

Physiological and behavioural studies of deterrent and attractant materials on oviposition of the desert locust, *(Schistocerca gregaria* Forskal).

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ABSTRACT

Contact chemoreception plays an important role on egg-laying behaviour and the rhythmic digging movements of the valves. Tested chemicals acted aversively and reduced both the duration spent egg-laying and the number of eggs laid, with the concentration at which they became aversive being dependent on whether the chemical was normally present in the diet. Chemicals such as glucose and sodium chloride prevented egglaying only at much higher concentrations than known methyl silicate and froth egg pods extracts. A chemical signal, originating from the froth of egg pods attracts gravid female *Schistocerca gregaria* (Orthoptera: Acrididae) to common egg laying sites. Behavioural experiments indicated that females preferred to oviposit in moist sand contaminated with froth (72 % egg laying 32% in sterilized sand). Extracts and volatiles collected from froth were also attractive to gravid females. In fact, froth volatiles elicited the strongest egg laying response (84% egg laying) compared with high concentration of glucose and NaCl. Results with froth extracts obtained by sequential extraction with solvents of increasing polarity suggest that both non-polar and polar compounds are involved in the attraction of gravid females. Electropysiological recordings with extracts collected from froth confirmed the presence of contact chemoreceptor receptors on the ovipositor that are responsive to compounds in the extracts. Similarly for animals in which fictive digging movements were induced all chemicals stopped the digging rhythm, with glucose and sodium chloride inhibiting the rhythm at relatively high concentrations compared to froth of egg pods and methyl silicate.

Keywords: Schistocerca gregaria; Oviposition; Froth of egg pods; Egg laying Electrophysiological.

INTRODUCTION

Many factors influence an insect's choice of egglavingsite. The range and types of potential egglaving sites are large and can include the undersides of leaves as in Lepidopterans (Simmonds, 2001; Rojas and Wyatt, 1999; Rojas et al., 2001), within the flesh of fruit as in fruit flies (Prokopy and Duan, 1998) or within soil or sandy substrates as in Orthopterans (Uvarov, 1977; Popov, 1980). To select appropriate egg-laying sites insects need to assess qualitative aspects of a substrate prior to and during egg-laying, including its surface characteristics, visual characteristics such as shape, and the presence or absence of certain chemicals (Hurter et al., 1999; Simmonds, 2001). All of these parameters can indicate the suitability of the substrate for egg-laying, which in turn may reflect the suitability of the substrate for offspring development (McCall and Cameron, 1995). In butterflies, the presence of flavonoids specific chemicals (e.g. and/or glucosinolates) on the leaves of a particular plant can indicate its identity and hence its suitability or unsuitability as a host for egg-laving (Simmonds, 2001). The sweet potato whitefly, Bemisia tabaci, for example, actively discriminates against older host leaves when attempting egg-laying (Veenstra and Byrne, 1998). The inability of an insect to make a

behavioural choice between suitable and unsuitable egg-laying substrates would compromise the survival of the resultant offspring (McCall and Cameron, 1995).

Contact chemoreception plays an important role in taste and dietary intake (Dethier, 1976; Simpson and Raubenheimer, 1993), avoiding potentially harmful chemicals in the environment (White and Chapman, 1990; Newland, 1998; Rogers and Newland, 2000; Newland et. al., 2000; Gaaboub, 2000 and Gaaboub, et. al., 2005) and in the location and selection of egglaying or oviposition sites as in Diptera (Degen and Städler, 1997), Orthoptera (Uvarov, 1977; Popov, 1980), Lepidoptera (Baur et al., 1998) and in Hymenoptera (Kuhlmann et al., 1998). The choice of an egg-laving site may often reflect an adult's choice of food. Female Lepidoptera select an egg-laying site, or host plant, that both they and their larvae preferentially feed upon (Baur et al., 1998). Egg laying and food sampling are closely linked and flies have been shown to exhibit various feeding related sampling behaviours on encountering a potential egglaying site (Degen and Städler, 1997). Drumming or scraping of the tarsi, palpating and biting movements of the mouthparts and probing movements of the antennae and egg-laying apparatus, the ovipositor, may all occur before a decision to accept or reject an

egg-laying site is made (Baur et al., 1998). Although it was recognised (Uvarov, 1977) that the suitability of an insect's egg-laying site depended on its physical composition.

Foam production in *S. gregaria* has been linked to secretions of the female accessory gland, but not in full. Accessory glands are derived from the apical end of the lateral oviducts, and are thought to consist of specialized secretory tissue involved in delivering secretions during egg laying. The suggested roles for the secretions are: foam formation, prevention of desiccation (Uvarov, 1977) and aggregation for oviposition (Saini et al., 1995). This foam also forms a plug which fills the space above the eggs in the egg pod and provides an escape route for the hatchling locusts.

Chapman (2003) and Rogers and Newland (2002) chemicals suggested that are functionally characterised by being aversive or phagostimulatory, in much the same way as has been hypothesised for vertebrates. Tousson and Hustert (2000a) showed that taste receptors, or basiconic sensillae, located on the locusts ovipositor respond physiologically to a variety of chemical stimuli, including chemicals that represent some of the basic taste qualities. Thus, locusts have the appropriate sensory apparatus on their abdomen to respond to the chemical constituency of the substrate and the sensory neurones that innervate the sensilla send their axons back to the terminal abdominal ganglion where they synapse with interneurones (Tousson and Hustert, 2000b) that may form part of the central pattern generating circuits that underpin digging and egglaying. Locusts lay eggs in damp sand or soil (Popov, 1980), and sequences of different behaviours occur before the decision to accept or reject an egg-laying site is made (Uvarov, 1977), as they do in flies. A sampling period that consists of probing, opening and closing movements of the ovipositor valves (Uvarov, 1977) superficially samples the surface of the substrate and provides the locust with information regarding the chemical and physical properties of the substrate. If the substrate is accepted at this stage, the rhythmic opening and closing movements of the ovipositor valves are accompanied by protractive and retractive movements that serve to elongate the abdomen by up to four times its original length and drive it into the substrate (Vincent and Wood, 1972; Jorgensen and Rice, 1983). This behavioural strategy appears unique to Orthopterans and serves to lay the eggs at depth, protecting them from desiccation, parasitisation and predation (Jorgensen and Rice, 1983). While Woodrow (1965) showed that different chemical types affected egg-laying, it is not clear whether chemicals influence behaviour in the same way as in feeding and dietary intake, or during avoidance related behaviours.

The aim of our study was to therefore determine whether there are simple basic principles for the categorisation of different chemicals across tasterelated behaviours or whether an animal will respond in different ways to the same chemical depending on the specific behaviour. Thus, our present studies illustrate some important questions as:

How the chemical composition of the substrate affects in the numbers of eggs laid?

How chemical stimulation affects the rhythmic movements of the ovipositor valves?

MATERIALS AND METHODS

Experimental insects:

All experiments were performed on sexually mature *Schistocerca gregaria* taken from our crowded laboratory culture conditions reared at 30 ± 2 °C under a 12h light / 12h dark regime and $65\pm5\%$ R.H. Hoppers were kept in wooden cages with glass sides (30x30x30cm) at a rate of 100 per cage (Hunter-Jones, 1961). It fed on fresh lettuce leaves. Prior to the dissection locusts were anaesthetised by cooling to 2-4°C and experiments were performed at 22-25 °C.

Extraction and testing of egg pod extracts (froth and eggs):

Froth and egg extracts were obtained either by sequential solvents extractions. For sequential extraction, eggs and froth derived from pods were allowed to dry at ambient temperature (25-27°C) for 6 h. Each part was then placed in a dropping funnel (50 ml) and 6 ml hexane added. After 10 min, the hexane extract was removed and the extraction repeated with ethyl acetate (6 ml) followed by methanol (6 ml). Single-solvent extractions of froth were carried out in the same way with hexane, ethyl acetate and methanol, each time using 25 ml of the solvents. The extracts were stored at -20°C until use. Amounts of extracts corresponding to 1 or 2 pod equivalents were tested individually or in combination in two- or four-choice bioassays Saini et al.1995.

Sand preparation

The sand of oviposition sites was sieved using wire mish $(2mm^2)$ and washed successively with hexane, ethyl acetate, methanol and finally with distilled water. It was then dried and heat-sterilized by baking in an oven at 150°c for 24 hrs. The ovipositing cups were filled with sterilized sand, the cups of the treated ovipositing females were contaminated with ethanol extracts, while the cups of the control was moisted by adding 15 ml water per 100 gm of sand (Saini *et al.*, 1995).

Electrophysiological studies:

The tip-recording technique (Hodgson *et al.*, <u>1955</u>) was used to record from the sensory neurons innervating both the tactile hairs (trichoid sensilla) and contact chemoreceptors (basiconic sensilla) on the paraproct. Before recording, tactile hairs were cut to approximately half their length, but basiconic sensilla were left intact.

Table 1: Mean Nr. of Egg Patch from froth egg pods extracts						
Conc.	Hexane	Ethyl acetate	Methanol	Water extract	control	
10%	1.7000	2.0000	3.0000	1.6000	2.0000	
7.5%	1.7600	2.0000	2.0000	3.6000	2.4000	
5%	2.0000	1.0000	3.0000	3.1600	2.2000	
2.5%	1.8000	1.0000	2.0000	2.6000	2.2000	
1.25%	1.8000	1.0000	2.0000	3.0000	2.0000	
Mean Nr. of Eggs from froth egg pods extracts						
10%	34.0000	33.0000	44.0000	43.0000	71.4000	
7.5%	43.0000	44.0000	45.0000	44.0000	74.6000	
5%	44.0000	43.0000	50.5000	54.0000	78.8000	
2.5%	54.0000	54.0000	65.0000	66.0000	77.8000	
1.25%	51.0000	55.0000	66.0000	66.0000	78.8000	
Mean % Hatching from froth egg pods extracts						
10%	66.3000	69.2000	73.2000	78.2000	95.0000	
7.5%	72.1000	74.2000	79.8000	83.6600	98.0000	
5%	73.0000	78.2000	83.1000	81.2000	96.3000	
2.5%	84.2000	83.2000	86.6600	83.4000	95.4000	
1.25%	85.1000	86.1000	86.6600	84.2000	97.2000	

Blunt glass recording microelectrodes containing 100 mM sodium chloride were then placed directly over the tips of the sensilla. The salt solution in the electrodes evoked spikes in some of the chemosensitive neurons, and movements of the electrode, which deflected the shafts of the sensilla, induced spikes in mechanosensory neurons (Newland et al., 2000).

RESULTS AND DISCUSSION

Biological response to different egg pods extracts:

Extracts were applied to the ovipositing sites of the ovipositing females, S. gregaria. Table (1) shows that, the numbers of egg pods, laid eggs, and hatched eggs of ovipositing female were reduced by exposure to the contaminated sand with egg pods extracts in hexane, ethyl acetate, methanol and water, respectively. The reduction was more pronounced in the egg pods extracts ovipositing female by exposure than control. The reduction percentages of hatched eggs and reproductive potential supported this conclusion, when ovipositing females were exposed to froth extracts (Figures 1-3). El-Gammal, et. al. (1983) found that the reduction percentages in reproductive potential of ovipositing solitary female were higher in the case of the application of gregary extracts to ovipositiong solitary females. Figures (1-3) indicates that, the effects of froth extracts and egg pod extracts on the reproductive parameters of ovipositing females were reduced the numbers of produced egg pods, laid and hatched eggs.

Our results agree with the results of El-Gammal, et. al. (1983) illustrate that, the obtained inhibitory actions of extracts of *S. gregaria* egg pods (froth and egg mass) on their reproductive parameters may be

induced as results of some disturbance in their haemolymph main metabolites.



Figure 1: The effects of different concentrations of egg pods extracts in mean Nr. of patch in female locust (*S. gregaria*).



Figure 2: The effects of different concentrations of egg pods extracts in mean % hatching in female locust (*S. gregaria*).



Figure 3: The effects of different concentrations of egg pods extracts in mean Nr. of eggs in female locust (*S.gregaria*).

So, it deemed necessary to disclose the biochemical situation in the haemolymph of the exposed ovipositing females, *S.gregaria* to these extracts.

The haemolymph main metabolites (proteins, carbohydrates, lipids and cholesterol) were affected in S. gregaria after their exposure to contaminated ovipositing sites with froth egg pod extracts of S. gregaria. El-Gammal, et. al. (1983) found the solitary ovipositing females were exposed to ethanol extracts of solitary froth, their heamolymph contents of proteins, carbohydrates cholesterol were reduced, while lipids contents were increased. On the other hand, when ovipositing gregary females exposed to ethanol extracts of solitary froth, their heamolymph contents of proteins and lipids were decreased while carbohydrates and cholesterol contents were increased. The biochemical effects of. gregary froth extracts on the haemolymph main metabolites of the exposed solitary or gregary ovipositing females. The haemolymph metabolites of the exposed solitary ovipositing females (proteins, lipids, and cholesterol) were increased while carbohydrate contents were decreased. The application of gregary froth extracts to the ovipositing site of ovipositing gregary females increased their haemolymph main metabolites than the control insects.



Figure 4: The effects of different concentrations of glucose in mean Nr. of patch in female locust (*S. gregaria*).

The biological results indicated that extracts of froth or egg masses were more effective. These extracts reduced the produced numbers of egg pods, laid eggs, hatched percentages and reproductive potential. The results of the chemical analysis supported these reductions because in most cases haemolymph main metabolites were disturbed to the levels which were insufficient to induce the normal numbers of egg pods, laid eggs and hatching percentages compared to those of the untreated control . These results are going in line with many other studies concerned with the action of Juvenile hormone (JH) and the anti - JH agents during maturation processes in *S.gregaria* (EL-Gammal, 1979 and 1983).

Table 2: The effects of different concentrations of glucose, Nacl and methyl silicate in mean Nr. of patch, Nr. of eggs and mean % hatching in female locust (*S.gregaria*).

Glucose						
Conc.	Mean Nr.	Mean Nr.	Mean %			
	of Patch	of Eggs	Hatching			
1500 mM	0.0000	0.0000	0.0000			
1000mM	0.4000	18.6000	42.0000			
500mM	0.8000	30.2000	66.0000			
250 mM	1.3000	49.8000	79.0000			
100 mM	1.5200	57.2000	84.0000			
Control	1.8000	71.8000	96.0000			
Nacl						
1000 mM	0.0000	0.0000	0.0000			
500 mM	0.0000	0.0000	0.0000			
250 mM	0.0000	0.0000	0.0000			
100 mM	1.2000	46.6000	81.0000			
50 mM	1.5000	64.2000	88.0000			
Control	1.9000	73.8000	96.4000			
Methyl silicate						
10%	0.9000	30.8000	54.2000			
7.5%	1.4000	39.0000	67.0000			
5%	1.7000	41.0000	69.0000			
2.5%	1.6000	51.0000	84.0000			
1.25%	1.2000	55.0000	88.0000			
Control	1.6000	69.4000	97.0000			



Figure 5: The effects of different concentrations of glucose in mean Nr. of eggs in female locust (*S* .*gregaria*).



Figure 6: The effects of different concentrations of glucose in mean % hatching in female locust (*S. gregaria*).



Figure 7: The effects of different concentrations of NaCl in mean % hatching in female locust (*S. gregaria*).



Figure 8: The effects of different concentrations of NaCl in mean Nr. of eggs in female locust (*S. gregaria*).



Figure 9: The effects of different concentrations of NaCl in mean Nr. of patch in female locust (*S. gregaria*).



Figure 10: The effects of different concentrations of methyl silcalte in mean Nr. of patch in female locust *(S. gregaria).*



Figure 11: The effects of different concentrations of methyl silcalte in mean Nr. of eggs in female locust *(S. gregaria).*



Figure 12: The effects of different concentrations of methyl silcalte in mean % hatching in female locust (*S. gregaria*).

Also, Highnam *and Haskell* (1964) stated that the yolk deposition in the terminal oocytes of *S. gregaria* requires JH. In this respect Chen *et al.* (1976) observed that vitellogenin synthesis was prevented in allatectomized emerged adults but cold be induced by topical application of C18–JH. Thus, the physiological and biochemical phenomena in *S. gregaria* are correlated with the required concentrations of JH. So, the impregnated ovipositing sites with ethanol extracts of froth or egg masses of

S.gregaria may be emitted some volatile compounds which may be disturbed JH concentrations in the exposed ovipositing females of both solitary or gregary phases. It was happened even that the gregarious female adults are known as a high content of JH than the solitarious ones (Tawfik *et al.*, 2000), who stated that, the biosynthesis of pheromone in *S.gregaria* is associated with a high JH peak in their haemolymph. Finally , the present findings are considered as a new approach of studies could be lead the researchers to generate some effective compounds from insects to suppress their reproductive potential as a novel approche for insects control .

Effect of different chemical composition on the number of egg pods laid: The greater the different chemical concentrations of the substrate provided for a locust the fewer the number of egg pods that were laid (Table 2). For all chemicals tested (NaCl, glucose and methyl silicate). Egg-laying was completely prevented at their higher concentrations, the exact concentration of which depended on chemical identity (Figures 4-12).

Macronutrients and anionic chemicals often found in a locusts' diet tended to stop egg-laying at concentrations higher than those chemicals that have been shown to act aversively or have anti-feedant effects (Rogers and Newland, 2000; White and Chapman, 1990). For example, locusts stopped laying eggs at a concentration of 1.5M glucose in the substrate compared to a 100 mM concentration (Rogers and Newland, 2000). Increasing the concentrations of three out of the three chemicals that are found in a locust's diet resulted in significant decreases in the number of egg pods being laid in the chemically treated test pots as in Table (2).

The results were defined as egg-laying in which the ovipositor valves initially made normal contact with the substrate, but were not followed by the abdomen being driven into the substrate. For all chemicals tested the number of egg pods laid divided by the number of egg laying attempts provided a measure of the percentage of egg-laying success. All chemicals test shows concentration dependent effects, with the percentage of unsuccessful attempts at egg-lay being greater the higher the concentration. Therefore the acceptance of substrate means that the female find the suitable oviposition sites and so, it starts to egg laid.

In butterflies, the presence of specific chemicals (e.g. flavonoids and/or glucosinolates) on the leaves of a particular plant can indicate its identity and hence its suitability or unsuitability as a host for egg-laying (Simmonds, 2001). The sweet potato whitefly, *Bemisia tabaci*, for example, actively discriminates against older host leaves when attempting egg-laying (Veenstra and Byrne, 1998). The inability of an insect to make a behavioural choice between suitable and unsuitable egg-laying substrates would compromise the survival of the resultant offspring (McCall and

Cameron, 1995). Female desert locusts preferentially lay eggs within damp sand (Popov, 1980). This is to ensure rigidity of the excavated hole, preventing the walls of the hole collapsing on the eggs and also to prevent their desiccation (Jorgensen and Rice, 1983). We show that the detection of chemicals within a substrate plays an integral part in the success of egglaying. Female locusts laid egg pods in sand pots containing low concentrations of all chemicals tested, although greater numbers of egg pods were laid in control pots. This suggests that the presence of low concentrations of chemicals in the substrate were detected. The concentration at which the chemicals acted aversively depended on the identity of the chemical while osmolarity and pH were not the major determinant of egg-laying success. This data closely parallels those of Rogers and Newland (2000), who showed a similar relationship between chemical type and the concentration ranges over which they became aversive.



Figure 13: Electrophysiological recording of different concentrations of glucose and NaCl on basiconic sensilla of ventral ovipositor valve.

The results suggests that, the egg-laying female locust has the appropriate sensory apparatus on the ovipositor valves to detect changes in the chemical composition of the substrate, and that this information can be used to modify the rhythmic digging movements of the ovipositior valves and abdomen. The same chemicals applied to the ventral surface of the ovipositor valves resulted in a cessation of the oviposition digging rhythm, and the duration for which the rhythm stopped depended on chemical type and concentration.

The electrophysiological studies indicate the suitable substances in the substrate were a marker fore the acceptance of oviposition (Fig. 13). Few studies have analysed the effects of chemosensory input on invertebrate central pattern generator (CPG) networks. In the pond snail *Lymnaea stagnalis*,

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chemical stimulation of the mouthparts with 100mM sucrose initiates rhythmic movements of the mouthparts (Kemenes et al., 1986).

In locusts glucose stimulation of the ovipositor valves resulted in inhibition of the oviposition digging rhythm, although high (1.5M) concentrations of glucose. In locusts, although the digging rhythm stopped immediately after chemical stimulation of the valves, the duration from chemical stimulation to reactivation of the digging rhythm was significantly longer for high concentrations of all chemicals. In addition, in locusts, on return of the digging rhythm following chemical stimulation the cycle frequency showed no significant difference compared to that of distilled water controls. Similarly in humans, the chewing frequency was not dependent on quinine concentration (Neyraud et al., 2005).

High concentrations of all chemicals were more aversive than low concentrations, and modified motor output by increasing the duration for which the oviposition rhythm stopped, showing very clear similarities with leg withdrawal movements (Rogers and Newland, 2000). Tousson and Hustert (2000b) showed that spiking local interneurones in the terminal abdominal ganglion respond to chemical stimulation of the ovipositor valves.

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