COMPTES RENDUS DU V[e] CONGRÈS

DE

L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX

Toulouse 5 - 10 Juillet 1965

Ouvrage publié avec le concours du Centre National de la Recherche Scientifique

LABORATOIRE D'ENTOMOLOGIE DE LA FACULTÉ DES SCIENCES

SYNCHRONISATION OF SEXUAL MATURATION IN DESERT LOCUST SWARMS

by D. B. CARLISLE and P. E. ELLIS
Anti-Locust Research Centre, London

Many suggestions have been made as to the selective advantage of swarm formation in locust, and while we do not wish to involve ourselves in the discussion as to what may be this selective advantage, it is at least clear that swarm formation represents a potent force for survival. Provided many hoppers of a similar age are to be found in a restricted area, their behaviour leads inevitably to group formation, which persists through larval life and is the genesis of the adult swarms. The behavioural aspects of this group formation were discussed by ELLIS at the last meeting of this union held in Pavia in 1961 (ELLIS, 1962). The occurence of large numbers of locust hoppers of a similar age in the field can only be the result of simultaneous hatching of large numbers of eggs which have been laid in close proximity to one another. This in turn is ensured by the simultaneous sexual maturation and gregarious oviposition of the locusts of any one parental swarm such as has been observed in the field by ELLIS and ASHALL 1957 and by POPOV 1958. NORRIS (1963) has analysed the behaviour of adult female laboratory locusts when about to lay. Such females are attracted to each other, but the chemical, tactile and visual inter-attractions between them serve to keep them together once they have met, rather than to attract them towards each other from some distance away.

It must be obvious that for simultaneous gregarious oviposition the females of the parental generation must have matured together. Where a swarm of Desert Locusts is feeding on lush green vegetation such more or less simultaneous oviposition is ensured by the direct maturation of the young locusts starting immediately after fledging and leading to egg laying within 3-4 weeks. But in many parts of its range the Desert Locust only breeds during the rainy season ant the gonads remain undeveloped during periods of drought. Before the rains commence the winds, in an area like the Somali Peninsula, become convergent on the Inter-Tropical Convergence Zone and serve to concentrate scattered populations of Desert Locust (SAYER 1962, RAINEY 1963, WALLOFF 1964). During the dry season in this area these locust will have remained for three months or more with undeveloped gonads and with the pink or beige colouration of the immature locusts. Yet within 2 or 3 weeks of their being concentrated in the Inter-Tropical Convergence Zone they are bright yellow and ovipositing in a gregarious manner.

One factor which would certainly tend to synchronise sexual maturation within swarms is the maturation pheromone which has been studied by NORRIS (1954) and LOHER (1960). These workers have demonstrated that mature male Desert Locusts produce a pheromone which stimulates the maturation of other individual of both sexes. It is also known that mature females produce the substance in a lesser amount and that males which have even begun to mature, though not yet reached the full yellow colouration of the sexually potent male, are already producing this maturation pheromone in small amount. This will have the result that once a few individuals have started to mature the rest of the swarm will tend to follow suit. In practical terms the, then problem of the analysis of the simultaneous maturation of the swarms comes down to an anlysis of the factors which start off maturation in a few individuals of the swarm, that is, factors which start off the chain reaction of maturation, propagated by the maturation pheromone. The other problem which analysis is that of the factors which serve to cause the delay in maturation of animals during the dry season. NORRIS 1957 has shown that for locusts reared in pairs maturation may be delayed under condittions of long day length, but this is clearly not only factor involved and is not effective for laboratory locusts reared in groups.

All our experiments have been performed upon adults of the Desert Locust (*Schistocerca gregaria* Forskål) bred for many generations in the laboratories of the Anti-Locust Research Centre in London.

DELAYED MATURATION

ELLIS, CARLISTE and OSBORNE (1965) have analysed the factors which contribute to the delay of maturation. In periods of infrequent rain in the desert the season of green vegetation is very short, so that although the young hoppers may be feeding upon lush green vegetation, by the time they fledge plants already have senescent and sere yellow leaves. Under these conditions when the young adults are feeding upon senescent vegetation they do not mature. In the laboratory we have found that a diet of senescent yellow leaves always leads to a long delay of two or more months in breeding. This is true even when temperature, humidity, photo-period and the presence of large numbers of other mature locusts are ideal for rapid maturation in the laboratory. Despite all these optimal conditions it may be three months before the first eggs are laid by locusts given an excess of yellow leaves to eat (*fig.* 2). It is easily shown taht this is not a shortage of water or of protein (*fig.* 2). It is, however, known that senescent leaves are short of the plant growth hormones. And

Fig. 1

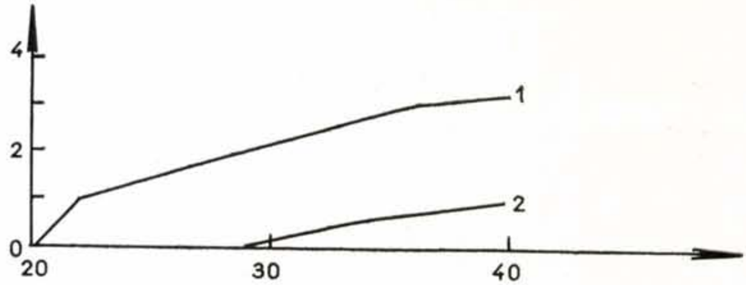

Fig. 2

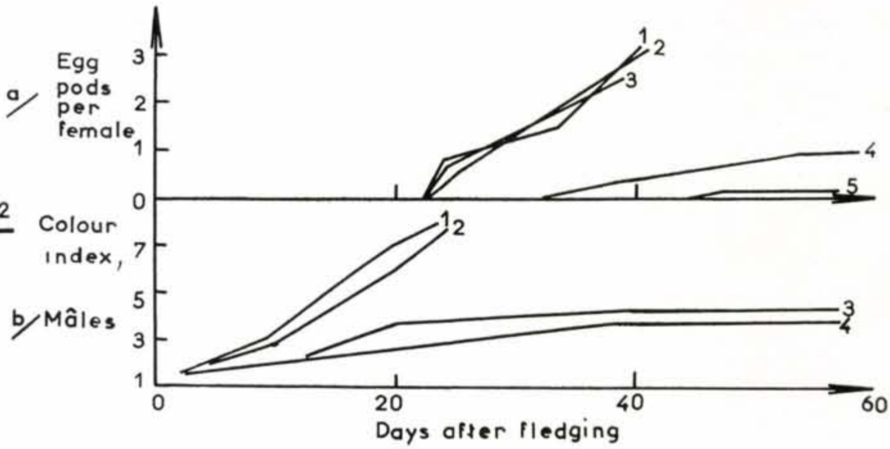

Fig. 3

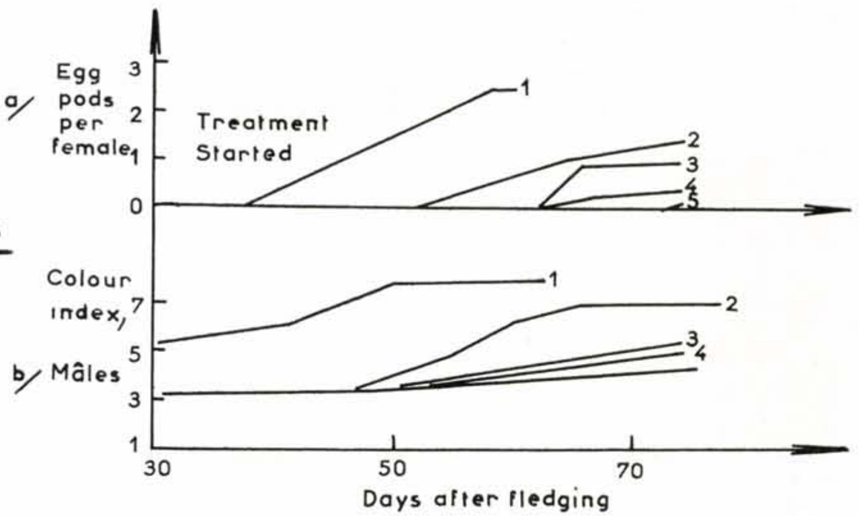

FIG. 1. — Green diet Reared in pairs.

1° Treated on day with myrrh oil. — 2° No treatment.
Abcisse : Egg pods per female — *Ordonnée :* Days after fledging.

FIG. 2. — Reared in groups.

a) 1° Yellow diet + Eugenol — 2° Yellow diet + GA — 3° Green diet — 4° Yellow diet + protein — 5° Yellow diet.
b) 1° Yellow diet + Eugenol — 2° Green diet and Yellow diet + GA — 3° Yellow diet + protein — 4° Yellow diet.

FIG. 3. — Reared in groups.

a) 1° Green diet — 2° Yellow diet + GA + Eugenol — 3° Yellow + Eugenol — 4° Yellow + GA — 5° Yellow diet.
b) 1° Green diet — 2° Yellow diet + GA + Eugenol — 3° Yellow diet + Eugenol — 4° Yellow diet + GA.

in the species of *Brassica* with which we have worked we have shown that gibberellins are in very short supply. We have therefore supplemented the diet of yellow *Brassica* leaves with gibberellin-A3 fed to the locusts on filter paper. On this régime of yellow vegetation supplemented with gibberellin from the day of fledging the locusts mature as quickly as if they were feeding on green leaves (*fig.* 2). Too high an intake of gibberellin on the other hand proves slightly inhibitory so that a large dose administered with yellow leaves or a smaller dose fed with green leaves both lead to a delay of a week or ten days in sexual maturation. On the other hand, if locusts are fed for a month after fledging on yellow vegetation without any dietary supplement, gibberellic acid added to the diet from this stage on has little effect (*fig.* 3). In other words a shortage of gibberellic acid in the yellow and senescent vegetation on which the locusts are feeding may be enough to prevent maturation of the gonads but an introduction of gibberellin to the diet in animals which have delayed maturation is not enough to initiate sexual maturation afresh.

Perhaps at this point we had better say what we use as criteria of maturation. As Desert Locusts mature they change colour from pink when they are newly fledged through buff or beige and finally to yellow. We can distinguish eight clearly definable stages in this colour progression and so we have established an index from one for the pink animal through to eight for the fully yellow mature locust. That is the first criterion of the progress of maturation. A second criterion in short term experiments consists in measuring the oocyte length in females which have been killed. A more satisfactory alternative, but one which involves more work and longer periods, is to keep the animals in pairs or small groups until they finally lay eggs; in this way we can obtain a plot of their egg laying performance, both when it starts and how frequently they lay eggs.

We know from the work on the maturation pheromone that Desert Locusts are able to respond to chemical cues for their sexual maturation. We know from field observations that the locusts start to mature with the first flush of green on the shrubs of the Desert. Now the first shrubs to come into leaf in most desert areas are all highly odoriferous and most of them have already dropped their leaves again before the locust hoppers of the next generation have reached the fifth instar. The odoriferous nature of the shrubs suggested to us the possibility that locusts may be responding to this chemical cue before the onset of the rains in the same way as they are able to respond to the chemical cue of the pheromone of the male. Preliminary analysis of this concept has been carried out by CARLISTE, ELLIS and BETTS (1965), who showed that indeed the essential oil of myrrh (*Commiphora* species, one of the major odoriferous genera of the East African deserts) will indeed hasten maturation in laboratory-fed Desert Locusts. These locusts were all fed a green diet and the oil was applied in microgram quantities externally as a single dose to the underside of the thorax on the second or third day after fledging (*fig.* 1). Locusts so treated matured a week or two earlier than the controls. Of the various fractions of the oil of myrrh it was found that eugenol was particularly active. This is a common constituent of the essential oils produced by many desert shrubs when they come into leaf and may thus be a factor in the initiation of maturation of locusts in many desert areas at the beginning of the rainy season.

It remained to be seen whether these oils were active upon animals which had been feeding upon senescent vegetation and had therefore shown a prolonged delay in maturation. In our most recent experiments we have found that a single dose of eugenol administered as before on the second or third day after fledging to locusts fed on yellow vegetation leads to maturation as soon as or sooner than in animals fed on green vegetation and much sooner than those fed on yellow vegetation (*fig.* 2). In another experiment locust were fed for a month on senescent vegetation and then some of them were treated with eugenol and were also given a supplement of gibberellic acid in the diet. Others received either one or other of these treatments (*fig.* 3). Gibberellic acid alone had a slight effect; eugenol alone initiated maturation and the animals started laying eggs some three weeks later. A combination of the two treatments however had a much more striking effect and all the animals so treated laid eggs by some three weeks after treatment.

To sum up we would suggest that locusts fledging at the beginning of the dry season and feeding on senescent vegetation failed to mature because of the shortage of the plant growth hormone gibberellin in their diet together with a concommitant shortage of monoterpenoids such as eugenol. The initiation of maturation at the end of the dry season would then depend partly on the reappearance of gibberellins in the diet, in the form of fresh green leaves of shrubs which appear just before the rains, and partly as a result of contact with the vapour of the essential oils given off by these odoriferous shrubs of the desert. It is note worthy in our experiments that exposure to these oils have led to synchronization of egg laying in treated animals. For instance, in one experiment in which the animals were reared in pairs, untreated females started laying on dates up to 18 days apart, while all females treated with a variety of monoterpenoids (Pinenes, eugenol, limonene) all started laying within 3 days of each other (see also the steepness of the initial part of the upper curves in *fig.* 2). This synchronization of oviposition and the even rate of development of the egg will then lead to simultaneous hatching of large numbers of eggs and hence to swarm formation in suitable conditions.