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A Migrant Pest in the Sahel: The Senegalese Grasshopper Oedaleus senegalensis [and Discussion]

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A migrant pest in the Sahel: the Senegalese grasshopper *Oedaleus senegalensis*

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The Senegalese grasshopper *Oedaleus senegalensis* is periodically a major pest of millet and other crops of subsistence agriculture in the Sahel zone of West Africa. Aspects of the species' biology are described. Eggs can survive several seasons and adults sometimes migrate up to 350 km per night, adaptations that contribute to the species' success in semi-arid areas. Evidence for migrations, both northwards with the S.W. monsoon and southwards with N.E. harmattan winds, is reviewed with particular reference to studies in Mali and Niger. Control strategies such as monitoring migrations and egg-laying to predict the sites of future outbreaks, possibly up to three years after heavy infestations, are considered.

1. Introduction

The Senegalese grasshopper *Oedaleus senegalensis* (Krauss) occurs in semi-arid grasslands in Africa, the Middle East and the Indian sub-continent (Batten 1969; Ritchie 1981; Popov 1988). The species is the most important grasshopper pest in the Sahelian zone of West Africa. This was not widely recognized until 1974 when, together with other grasshopper species, it infested 3500×10^3 ha† in West Africa and was responsible for the loss of 368000 tonnes of agricultural production (Bernardi 1986). *O. senegalensis* has recurred as a major pest, notably in 1975, 1977, 1985, 1986 and 1989. During 1986, insecticides were sprayed from aircraft and by ground applications on 3385500 ha of grasshopper-infested zones between Sénégal and Chad (FAO 1987*a*). The most intensive spraying, involving four DC-7 airplanes in Sénégal, Mali, Mauritania and the Gambia at a cost of 2700000 U.S. Dollars, was reported to have restricted crop losses to 5% (Walsh 1986), but this may be an over-optimistic estimate (N. D. Jago, personal communication).

With a preference for sandy soils, ideal for its egg-laying (see, for example, Cheke *et al.* 1980*b*), *O. senegalensis* feeds preferentially on grasses such as *Cenchrus biflorus* and *Aristida mutabilis* in savannas where these plants predominate. However, *O. senegalensis* is catholic in its choice of grass (Boys 1978) and often ravages millet and other crops grown by subsistence farmers (Cheke *et al.* 1980*a*; Centre for Overseas Pest Research (C.O.P.R.) 1982). Both nymphs and adults will consume the leaves and seed heads of millet plants, particularly when the latter are in the milky stage of grain formation. Attacks on seedlings, usually early in the season, may force farmers to sow again.

O. senegalensis can disperse over distances of up to at least 350 km during one night (Riley & Reynolds 1979) and is capable of surviving in the egg stage for at least three years (Fishpool & Cheke 1983). These adaptations for life in dry environments contribute to its success and pest status. This paper summarizes what is known of the species' ecology with emphasis on migrations within the Sahelian zone of West Africa and implications for control strategies.

† 1 hectare = 10^4 m^2.

2. Life cycle in West Africa

(a) Eggs

In West Africa nymphs can be found between March and November and adult *O. senegalensis* occur between April and December (Fishpool & Popov 1984). The intervening dry season is spent underground in the egg stage, with up to 45 and an average of about 25 eggs per pod (Launois-Luong 1979; Cheke *et al.* 1980*b*). Commonly, females lay twice, rarely three times, with five or six days between ovipositions (Launois-Luong 1979). The pods are usually aggregated, with densities of up to 13 pods m^{-2} (Popov 1980). The eggs may be attacked by a variety of predators, particularly larvae of Diptera (Bombyliidae) and Coleoptera (Histeridae, Meloidae and Tenebrionidae) (Cheke *et al.* 1980*b*; Popov 1980).

The time taken for the eggs to develop is complex, depending on the time of year, whether the eggs are in diapause or not and the rainfall. Not all the eggs in a pod will hatch with the first rains of the season. Laboratory experiments on the hatching of field-laid eggs showed clearly that the times taken to hatch eggs within a particular pod were highly variable, even when the whole pod was subjected to the same temperature (constant 30 °C) and humidity conditions. The shortest interval between a pod being moistened and the hatching of the first egg was 11 days (Cheke *et al.* 1980*a*), but the longest was 901 days (Fishpool & Cheke 1983). Hatching was protracted in all the pods studied, with a maximum of 1214 days (3 years and 4 months) elapsing between the hatching of the first and last eggs from the same pod (Fishpool & Cheke 1983). Thus, some eggs may not hatch until three wet seasons after they were first laid. There is also field evidence of viability after as long as five years (Saraiva 1962).

The pods used in the hatching experiments (Cheke *et al.* 1980*a*; Fishpool & Cheke 1983) had all been laid at the end of a wet season, but those laid at other times of the year may not include any diapausing eggs (Popov 1980). Nevertheless, these may also survive, quiescent, for three months in the absence of rain (Launois & Launois-Luong 1988). It is thought that decreasing day-length from September onwards, initiates the laying of diapausing eggs (Popov 1980). The variability in egg-laying and hatching behaviours is not only an adaptation for survival in habitats where the rainfall is erratic and patchy, but is also an insurance against isolated showers that are not followed by enough rain to maintain food supplies for the hoppers.

(b) Nymphs and adults

The nymphs can be serious pests, especially early in the wet season when they attack millet seedlings. There are five hopper instars, taking about three weeks to reach adulthood after eclosion, but as short a span as 15 days has been recorded in Mali in 1978 (Fishpool 1982) and in 1986 (N. D. Jago, personal communication). Accelerated rates of development contribute to increases in the intrinsic rate of natural increase of Desert Locusts *Schistocerca gregaria* (Forskål) (Cheke 1978) and may also play an important part in *O. senegalensis* outbreaks.

There have been reports of gregarious behaviour by *O. senegalensis* nymphs, including marching bands (Joyce 1952; Descamps 1953; Batten 1969; Popov 1988) whose members appear darker than solitary nymphs (Popov 1988; N. D. Jago, personal communication), but there is no unequivocal evidence for a phase change other than behavioural. Although both nymphs and adults can occur as either green or brown forms and a melanic form occurs in the Cape Verde Islands (Ritchie 1978), the proportion of each is seemingly under environmental control. Figure 1 shows how the percentage of brown adults at Watagouna (15° 15′ N,

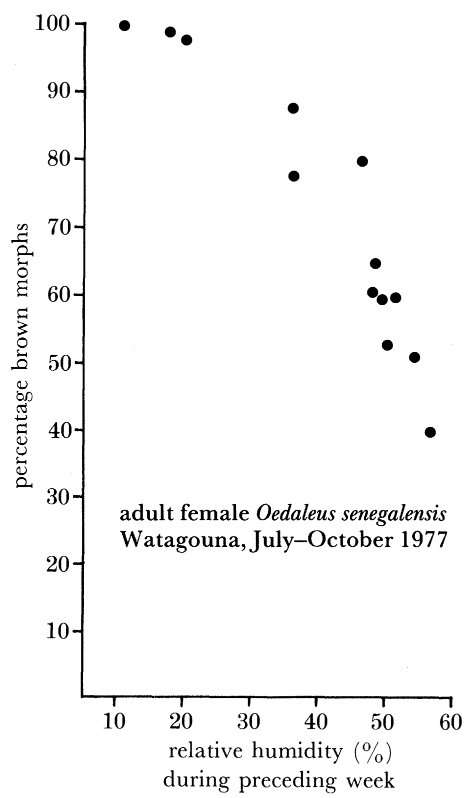

FIGURE 1. The percentage of brown morphs among collections of adult female *Oedaleus senegalensis* (sample sizes ranging from 9 to 1052) at Watagouna, Mali, during July–November 1977, in relation to the average relative humidity in the week preceding the collection (the averages of daily readings taken between 17h00. and 18h30.).

00° 43′ E) in Mali, during the 1977 season was inversely related to the humidity in the preceding week. This result, using field data, concurs with Rowell (1971) who said in his review of the subject that 'there is general agreement that humidity is the most important single factor in predisposing experimental populations in favour of the green morph.' However, it contrasts with a laboratory study in which only light and not temperature or humidity affected the colour of *O. senegalensis* (Abushama & El Khider 1973). Morphometric evidence for phase changes is also lacking. There was very little variation in the tegmen:femur ratio of adult females at Niamey, Niger (13° 31′ N, 02° 07′ E) during August–November 1977 (figure 2). Similar results were found for both tegmen:femur and tegmen:caput ratios at Danga (14° 31′ N, 01° 56′ E) in Niger in August–September 1974 during a serious outbreak of *O. senegalensis* (J. M. Ritchie, personal communication). However, Bhatia & Ahluwalia (1967) found a shift from a tegmen:femur ratio of 1.68 in an area where no concentrated breeding occurred to one of 1.73 where there was such breeding, but only 47 insects were measured.

After the final moult adult females take about ten days to reach maturity and become capable of egg-laying (Launois 1978; Fishpool 1982). There is evidence that if they are going to disperse most do so before maturing (Jago 1979; Riley & Reynolds 1983). Cheke *et al.* (1980*a*) found that females caught in light traps were more than three days old but many were six or more days old. Such samples consisted mostly of young adults, with immature ovaries, or females that had just laid, whereas samples netted in adjacent fields had more mixed age

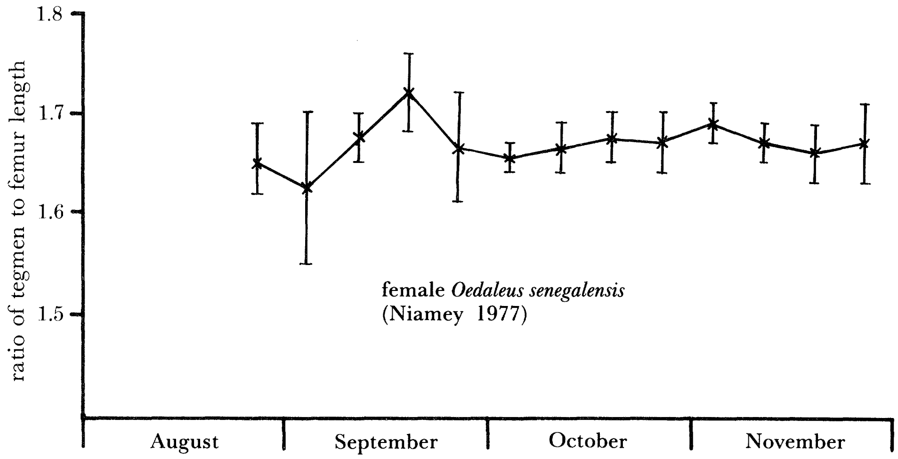

FIGURE 2. The ratio of tegmen length:femur length of female *Oedaleus senegalensis* caught at Niamey during August–November 1977. The vertical lines are 95% confidence limits about the mean values.

structures including gravid insects. There are no accounts of cohesive adult swarms, but flights of loose aggregations have been seen (Bhatia & Ahluwalia 1967; Batten 1969; Ahluwalia *et al.* 1976; Popov 1976; Lecoq 1978*a*), and sometimes steady drifts of short flights in one direction have been noted (N. D. Jago, personal communication). Most migrations probably take place at night.

3. Migration

(*a*) *Evidence for northward movements with S.W. monsoon winds*

The evidence for northward movements, by which I mean any displacements north of the source, including those with N.E. or N.W. biases, is more circumstantial than is the case for southward migrations. Northward movements would be expected when the Inter-Tropical Convergence Zone (ITCZ) is north of the grasshoppers and the prevailing winds are southerlies or south-westerlies. Southward migrations including those with S.W. or S.E. biases, will tend to occur when the ITCZ is south of the insects and the prevailing winds are the dry, warm, generally N.E. 'Harmattan' winds. These are, of course, generalizations and events will often be determined by smaller scale phenomena such as storms and other disturbances.

There are three possible reasons for the paucity of data on northward movements. One is that they may not occur regularly. Another is that few intensive studies have been conducted at the beginning of the rainy seasons, when southerly winds predominate. Finally, adult populations will tend to be smaller and less easy to detect at this time. However Lecoq (1978*b*) noted that a population of up to 360 adults per hectare at Saria (12° 53′ N, 02° 19′ W) in Burkina Faso, on 17 June 1976 had all but disappeared three days later (with no evidence for a sudden mass mortality) and he inferred that they had emigrated north with the advancing rains. N. D. Jago (personal communication) observed a mass influx of grasshoppers, including *O. senegalensis*, at Mourdiah in Mali (14° 28′ N, 07° 28′ W) on 29–30 June 1986. The first heavy rains of the year (37 mm) also fell during the same night and there were no substantial populations north of Mourdiah, suggesting a movement from the south. The grasshoppers remained, at a density of 5 m^{-2}, for three days and left abruptly on 3 July during a night of further rainstorms. A similar northward movement, of about 50 km, was noted at Hombori (15° 16′ N, 01° 40′ W) in Mali during June 1985 (Popov 1988).

Reynolds & Riley (1988), by using radar, documented a north-eastward movement of grasshoppers, including *O. senegalensis*, on 10–11 October 1978 near Gao (16° 16′ N, 00° 03′ W) in Mali. This occurred when the ITCZ was north of the insects, and the prevailing winds were south-westerlies. Similar events were recorded on other nights (D. R. Reynolds, personal communication).

(*b*) *Evidence for southward movements with NE Harmattan winds*

In October 1974, there was evidence for a southward movement in Nigeria. Between 5 and 15 October, there were high densities of adult *O. senegalensis* at Maiduguri (11° 53′ N, 13° 16′ E) with a maximum noted on the night of 10 October. On 12 October they began to be recorded at latitude 11° 15′ N, 250 km further south (Popov 1976).

Lecoq (1978*c*) recorded an influx into his Saria study site in October 1975, which culminated with densities of 1000 adults per hectare. He concluded that these were immigrants as no soft-bodied juveniles were noted, only grasshoppers with hard integuments, and catches at light were abundant.

During the last week of September 1977 there were reports of heavy *O. senegalensis* infestations in the Maradi (13° 28′ N, 07° 06′ E) and Zinder (13° 48′ N, 08° 59′ E) regions of southern Niger and in northern Nigeria (Cheke *et al.* 1980*a*). At the time a line of light traps, supplemented by ground surveys, was maintained along the length of the Niger river from Gao, in Mali, southeast through Niger to Malanville (11° 52′ N, 03° 24′ E) in Benin. At one of these sites, Niamey, the trap catch reached 4416 *O. senegalensis* on the night of 3 October, when there was no interference from moonlight. This was the first catch of the season in excess of 1000 and presaged an influx of unprecedented proportions, culminating in a peak of 15030 on 13 October. Figure 3 shows the position of the ITCZ at mid-day on 1, 2, 3 and 4 October in relation to records of high-density occurrences of adult *O. senegalensis* during the period 2–5 October and areas where the species was known to cause damage to millet (*Pennisetum americanum*). These data provide good circumstantial evidence of grasshopper movements in relation to those of the ITCZ. Figure 4 shows a possible reason for the mass movement: during September the rainfall had been half the average in the most heavily infested areas, rendering the habitats inimical to *O. senegalensis*. The drought conditions, by forcing the grasshoppers out of desiccating grasslands into comparatively lush millet fields, may also have accounted for the crop damage.

The strongest evidence for *O. senegalensis* migrations is provided by the radar studies of Riley & Reynolds (1979, 1983). In the earlier paper they describe how they observed targets with wingbeat frequency 'signatures' corresponding to those of *O. senegalensis* flying S.W. over the 'middle Niger' area of Mali. Back trajectories showed that the insects were often travelling at least 50 km in a night and sometimes as far as 350 km. In 1978, two radars were deployed in the Gao area of Mali. On the night of 21 October a dense concentration of targets, with the characteristics typical of *O. senegalensis*, overflew one radar and was then detected only two hours later by the second radar positioned 100 km further south (Riley & Reynolds 1983).

Ritchie (1978) documented catches at sea up to at least 100 miles off the west African coast and concluded that in nearly all cases the insects had been blown offshore by easterly winds.

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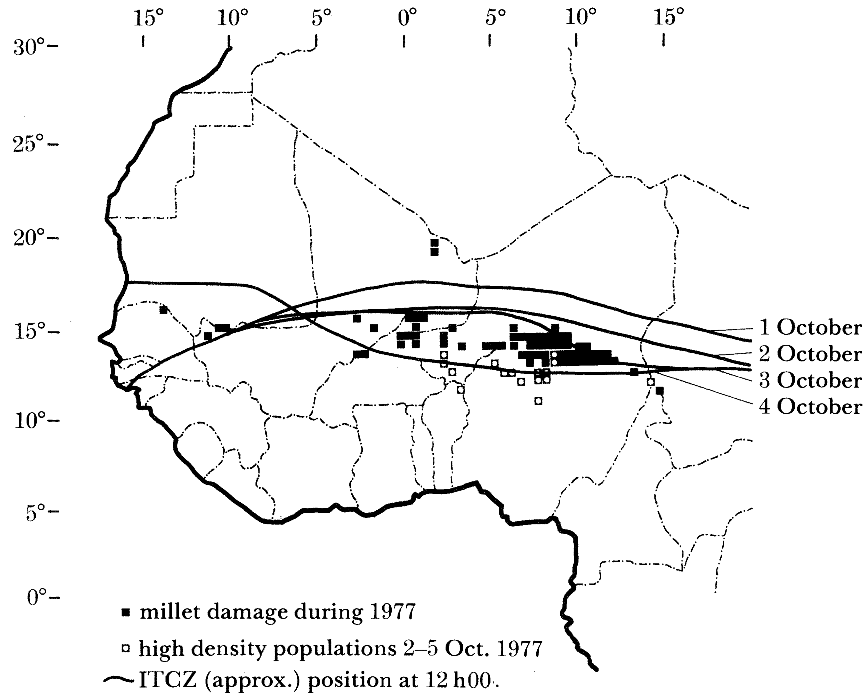

FIGURE 3. The position of the Inter-Tropical Convergence Zone at mid-day on 1, 2, 3 and 4 October 1977 an occurrence of *Oedaleus senegalensis* in the region. Closed symbols, sites where millet was damaged by *Oe senegalensis* during 1977; open symbols, sites where high density populations were suddenly recorded during October 1977.

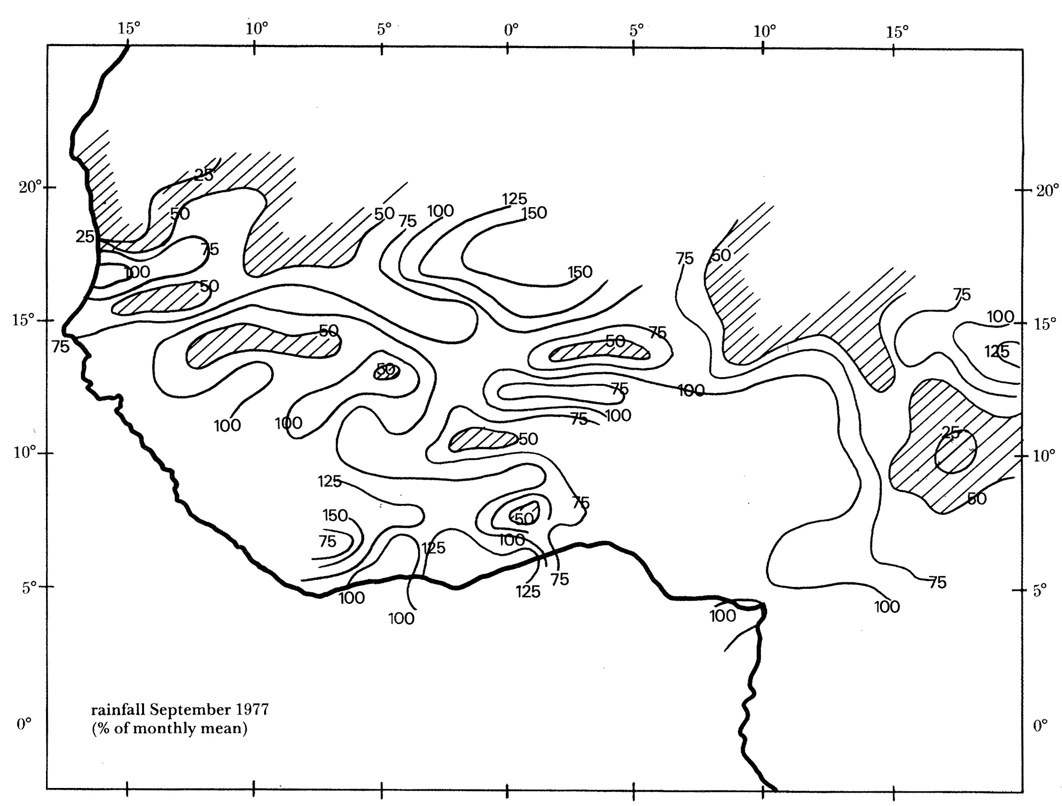

FIGURE 4. The rainfall in West Africa during September 1977 expressed as a percentage of the September monthly mean. (The shaded areas highlight zones with less than 50%.)

In exceptional circumstances *O. senegalensis* may be blown as far as the Cape Verde Islands, a distance of 600 km or more.

4. Significance of migrations

Given a period of about six weeks to complete a life cycle in the wet season, three or four generations may occur in one season. Launois (1979), incorporating these figures, proposed a scheme whereby each of three 'generations' were associated with different ecological zones, according to rainfall and the movements of the ITCZ. He suggested that there was an 'area of initial multiplication' between the annual rainfall isohyets of 1000 and 750 mm where development occurs at the beginning (April and May) and end (November) of the wet season. Emigrants from the April and May populations fly north to the 750 to 500 mm isohyet belt (the 'transitional area of multiplication') where, during June and July, they mix with locally bred insects derived from eggs laid in that region in the previous season. These in turn provide more northward migrants which reinforce populations hatching in the 500 to 250 mm rainfall belt (the 'northern area of multiplication'), during August and September. Finally, there is a southward migration from August to October through all three zones, thus completing the cycle.

As a simple summary of aspects of the species' phenology, Launois' scheme has been followed by others (see, for example, Popov 1988) but it does not allow for events such as: (i) extensive hatching in any zone at any time, if rain falls on eggs laid in previous seasons: (ii) the vagaries of the ITCZ and mesoscale wind convergences that may lead to movements in directions other than those predicted and, (iii) up to three generations following each other successively in the same site or zone, as shown by Fishpool (1982) at Watagouna. Indeed Fishpool noted that in 1978, taking account of all his study area, there were four generations.

Predictive algorithms derived from Launois' scheme, which use indices to effect changes at ten-day intervals, exist (Arnaud *et al.* 1982; Launois 1979, 1984; Bernardi 1986; Launois & Launois-Luong 1988; Lecoq 1989). Environments are classified into up to 36 categories on the bases of photoperiod (day-length more or less than 12 h), mean temperature, humidity (ratio of actual to potential evapotranspiration) and a 0–5 index of vegetation turgidity. The responses of *O. senegalensis* eggs, nymphs or adults within a particular environment are scored according to a set of scaled indices representing speed of development, survival and 'success' (defined as the product of the other two indices). The score for a particular geographical area will depend on: (i) its environment category: (ii) a combination of current and historical values of rainfall, temperature, and potential evapotranspiration and (iii) a mean index for the *O. senegalensis* populations at the end of the preceding dry season. Migration is represented by populations being carried in or out of a zone dependent on whether the environment is or is not favourable to the grasshoppers becoming sedentary, according to a scale from 0 (no displacement) to 5 (maximum flight activity). Finally the simulation plots maps of areas with different degrees of risk in terms of densities of egg-pods, nymphs or adults. The densities are scaled from 1 to 5. For nymphs 1 is a negligible density (less than 0.1 per m^{-2}) and 5 is high (more than 30 per m^{-2}). Thus the simulations do not use quantitative data on the grasshoppers' biology, and the only meteorological information that they include (other than that embodied in the definition of environment categories) are details of rainfall, temperature and potential evapotranspiration. Nevertheless, it is claimed that predictions are correct in 70–80 % of cases when attempts have been made at validation (Launois & Launois-Luong 1988).

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The accuracy of the computer simulations would be improved if they assessed more critically the effects of local meteorological conditions on grasshopper migrations, instead of depending, as they appear to do, on the notion of a shift in the species' 'centre of gravity' in line with movements of the ITCZ as each season progresses. Furthermore, they omit important biological attributes: for instance, Arnaud *et al.* (1982) ignored eggs surviving more than one season on the grounds that the experiments of Cheke *et al.* (1980*a*) were unrealistic. Arnaud *et al.* (1982) argued that it is normal to have an extended hatching period with a constant temperature of 30 °C, as the breaking of diapause with time is always more progressive and less synchronous than diapause broken by cold spells. However, many of the eggs studied by Cheke *et al.* (1980*a*), including one which did not hatch until 413 days after its first wetting, were collected in February 1978 and so would have experienced cold spells in the field. Furthermore, Venkatesh *et al.* (1972) conducted experiments at different temperatures and concluded that water was responsible for the termination of *O. senegalensis* diapause, irrespective of the temperature at which the eggs were kept. Launois & Launois-Luong (1988) acknowledged that diapausing eggs can survive a year or more in the complete absence of rain, but ignore the possibility that they may not hatch even when rained on: the laboratory egg experiments showed that even with an abundance of water, some eggs may not hatch for many months or years. The diapause has had applied importance: Saraiva (1962) described how there was a major outbreak on Boa Vista in the Cape Verde Islands in 1948 after five Senegalese grasshopper-free years; and an upsurge in Mali in 1985 and 1986 was ascribed to the accumulation of eggs over successive years (Steedman 1988). Although the contribution of diapausing eggs to outbreaks requires evaluation, it should not be ignored as it may be as significant as migration.

5. Control

As both nymphs and adult *O. senegalensis* can damage crops, the ideal control strategy would be the elimination of nymphal populations before the grasshopper numbers build up excessively and long-distance movements take place. However, this would require a rapid response on an extensive scale. An alternative would be to predict where extensive hatching will take place on the basis of the knowledge of previous seasons' laying activities and current rainfall patterns. This approach has already been recommended (FAO 1987*b*) and is current practice in some areas (FAO 1987*a*). Even if influxes of grasshoppers at the end of seasons do not cause any damage, knowledge of the migrations of *O. senegalensis* is important so that places where large numbers of grasshoppers may have laid can be surveyed to aid the plans for subsequent control interventions.

It is not yet clear if high populations of *O. senegalensis* always require control, for strategic purposes, or whether they can be tolerated under some circumstances. Most of the mass migrations occur in October at the end of the season and in some cases this is after crops have already been harvested, so control of such populations could only be justified as a strategic measure to minimize egg-laying. There is some evidence, including the events of 1977 described above, to suggest that the grasshoppers move out of their preferred pastures into cultivated land when the former become excessively dry. It may also be only under such circumstances, when drought conditions have forced them to seek more amenable areas to feed or oviposit, that the grasshoppers migrate. Thus, there may be times when although high populations are thriving in grasslands they do not need controlling as they are not threatening crops. If this is often the case, then a good strategy would be to issue farmers with facilities such as ultra low volume spraying equipment or supplies of insecticide-impregnated bran for them to use as necessary, rather than the organization of mass spraying campaigns involving aircraft. However, when massive upsurges occur it is most unlikely that such small-scale control efforts could stem the tide of invading grasshoppers.

The possibilities for identifying aerial target populations, once migrations have started, by airborne radar are discussed elsewhere in this volume (Pedgley, this symposium; Riley & Reynolds, this symposium).

To date, control has relied on ground and aerial applications of insecticides. Henry *et al.* (1985*a*) reported that in trials of applying the microsporidian parasite *Nosema locustae* Canning, *O. senegalensis* took up the spores and is probably susceptible to infection by *Nosema*. Other more virulent pathogens have also been isolated from *O. senegalensis* (Henry *et al.* 1985*b*) and so there are possible alternatives to insecticide use, which merit further trials.

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References

Abushama, F. T. & El Khider, E. T. M. 1973 Colour change in the grasshopper *Oedaleus senegalensis* Krauss (Fam. Acrididae). *Z. angew. Ent.* **72**, 415–421.

Ahluwalia, P. J. S., Sikka, H. L. & Venkatesh, M. V. 1976 Behaviour of swarms of *Oedaleus senegalensis* Krauss Orthoptera: Acrididae-subfamily-Oedipodinae. *Indian J. Entomol.* **38**, 114–117.

Arnaud, M., Forest, F. & Launois, M. 1982 Automatisation d'un modèle écologique original propre à *Oedaleus senegalensis* (Krauss 1877) (Orthoptera, Acrididae). *Agron. trop.* **37**, 159–171.

Batten, A. 1969 The Senegalese grasshopper *Oedaleus senegalensis* Krauss. *J. appl. Ecol.* **6**, 27–45.

Bernardi, M. 1986 Le problème des sauteriaux. In Compte-Rendu du Séminaire International du Projet CILSS de Lutte Integrée, Niamey (Niger) 6–13 December 1984, pp. 43–57.

Bhatia, D. R. & Ahluwalia, P. J. S. 1967 *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae-subfamily Oedipodinae) plague in Rajasthan (India). *Pl. Prot. Bull., New Delhi* **18**, 8–12.

Boys, H. A. 1978 Food selection by *Oedaleus senegalensis* (Acrididae: Orthoptera) in grassland and millet fields. *Entomologia expl. appl.* **24**, 278–286.

Cheke, R. A. 1978 Theoretical rates of increase of gregarious and solitarious populations of the desert locust. *Oecologia* **35**, 161–171.

Cheke, R. A., Fishpool, L. D. C. & Forrest, G. A. 1980*a* *Oedaleus senegalensis* (Krauss) (Orthoptera: Acrididae: Oedipodinae): an account of the 1977 outbreak in West Africa and notes on eclosion under laboratory conditions. *Acrida* **9**, 107–132.

Cheke, R. A., Fishpool, L. D. C. & Ritchie, J. M. 1980*b* An ecological study of the egg-pods of *Oedaleus senegalensis* (Krauss) (Orthoptera: Acrididae). *J. nat. Hist.* **14**, 363–371.

C.O.P.R. 1982 *The locust and grasshopper agricultural manual.* London: Centre for Overseas Pest Research.

Descamps, M. 1953 Observations relatives au criquet migrateur Africain et à quelques autres espèces d'Acrididae du nord Cameroun. *Agron. Trop.* **6**, 576–614.

F.A.O. 1987*a* Migrant Pest Newsletter (nos. 51–52), 1987. Rome: FAO.

F.A.O. 1987*b* *FAO guidelines for egg-pod surveys with special reference to the Senegalese grasshopper Oedaleus senegalensis* (Kr.), *1987*. Rome: FAO.

Fishpool, L. D. C. 1982 The ecology of the West African grasshopper fauna of the Sahel and sudan savanna with special reference to *Oedaleus senegalensis* (Krauss 1877). Ph.D. thesis, University of London.

Fishpool, L. D. C. & Cheke, R. A. 1983 Protracted eclosion and viability of *Oedaleus senegalensis* (Krauss) eggs (Orthoptera, Acrididae). *Entomologists mon. Mag.* **119**, 215–219.

Fishpool, L. D. C. & Popov, G. B. 1984 The grasshopper faunas of the savannas of Mali, Niger, Benin and Togo. *Bull. Inst. fondam. Afr. noire* **43**, 275–410.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Henry, J. E., Fowler, J. L., Wilson, M. C. & Onsager, J. A. 1985*a* Infection of West African grasshoppers with *Nosema locustae* Canning (Protozoa: Microsporida: Nosematidae). *Trop. Pest Mgmt*, **31**, 144–147.
Henry, J. E., Wilson, M. C., Oma, E. A. & Fowler, J. L. 1985*b* Pathogenic micro-organisms isolated from West African grasshoppers (Orthoptera: Acrididae). *Trop. Pest Mgmt*, **31**, 192–195.
Jago, N. D. 1979 Light trap sampling of the grasshopper *Oedaleus senegalensis* (Krauss, 1877) (Acrididae; Oedipodinae) and other species in West Africa: a critique. *Proc. 2nd. Trienn. Meet. (21–25 July 1979)*, pp. 165–198. Pan American Acridological Society, Bozeman, Montana, U.S.A.
Joyce, R. J. V. 1952 The ecology of grasshoppers in East Central Sudan. *Anti-Locust Bull.* **11**.
Launois, M. 1978 Modélisation écologique et simulation opérationelle en Acridologie. Application à *Oedaleus senegalensis* (Krauss, 1877). *Ministère de la Cooperation, Paris.*
Launois, M. 1979 An ecological model for the study of the grasshopper *Oedaleus senegalensis* in west Africa. *Phil. Trans. R. Soc. Lond.* B **287**, 345–355.
Launois, M. 1984 Les bio-modèles à géométrie variable appliqués à la surveillance des criquets ravageurs. *Agron. trop.* **39**, 269–274.
Launois, M. & Launois-Luong, M. H. 1988 *Oedaleus senegalensis* (Krauss, 1877) sauteriau ravageur du Sahel. Collection Acridologie Opérationelle. 3. *Ministère des Affaires Etrangères des Pays-Bas, La Haye et CIRAD/PRIFAS, Montpellier.*
Launois-Luong, M. H. 1979 Etude de la production des oeufs d'*Oedaleus senegalensis* (Krauss) au Niger (Région de Maradi). *Bull. Inst. fondam. Afr. noire* **41**, 128–148.
Lecoq, M. 1978*a* Le problème sauteriaux en Afrique soudano-sahélienne. *Agron. trop.* **33**, 241–257.
Lecoq, M. 1978*b* Les déplacements par vol à grande distance chez les Acridiens des zones Sahélienne et soudanienne en Afrique de l'Ouest. *C. r. Acad-Sci., Paris* (D) **286**, 419–422.
Lecoq, M. 1978*c* Biologie et dynamique d' un peuplement acridien de zone soudanienne en Afrique de l' Ouest (Orthoptera, Acrididae). *Annls. Soc. ent. Fr.* (N.S.) **14**, 603–681.
Lecoq, M. 1989 Les biomodèles en Acridologie et leurs applications opérationnelles. In *Report of the meeting on desert locust research: defining future research priorities*, pp. 82–99. Rome: FAO.
Popov, G. B. 1976 The 1974 outbreak of grasshoppers in Western Africa. In *Report of the Sahel Crop Pest Management Conference, held at the invitation of the Agency for International Development, United States Department of State, Washington DC, USA, December 11–12, 1974* (ed. R. F. Smith & D. E. Schlegel), pp. 35–43. Berkeley: University of California (for United States Agency for International Development).
Popov, G. B. 1980 Studies on oviposition, egg development and mortality in *Oedaleus senegalensis* (Krauss), (Orthoptera, Acridoidea) in the Sahel. Centre for Overseas Pest Research. *Misc. Rep.* **53**.
Popov, G. B. 1988 Sahelian grasshoppers. *ODNRI Bull.* **5**.
Reynolds, D. R. & Riley, J. R. 1988 A migration of grasshoppers, particularly *Diabolocatantops axillaris* (Thunberg) (Orthoptera: Acrididae), in the West African Sahel. *Bull. ent. Res.* **78**, 251–271.
Riley, J. R. & Reynolds, D. R. 1979 Radar-based studies of the migratory flight of grasshoppers in the middle Niger area of Mali. *Proc. R. Soc. Lond.* B **204**, 67–82.
Riley, J. R. & Reynolds, D. R. 1983 A long-range migration of grasshoppers observed in the Sahelian zone of Mali by two radars. *J. Anim. Ecol.* **52**, 167–183.
Ritchie, J. M. 1978 Melanism in *Oedaleus senegalensis* and other Oedipodines (Orthoptera, Acrididae). *J. nat. Hist.* **12**, 153–162.
Ritchie, J. M. 1981 A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae). *Bull. Br. Mus. nat. Hist. (Ent.)* **42**, 83–183.
Rowell, C. H. F. 1971 The variable coloration of the acridoid grasshoppers. *Adv. Insect. Physiol.* **8**, 146–198.
Saraiva, A C. 1962 Plague locusts – *Oedaleus senegalensis* (Krauss) and *Schistocerca gregaria* (Fôrskal) in the Cape Verde Islands. (In Portuguese with English summary.) *Estudos agron.* **3**, 61–89.
Steedman, A. (ed). 1988 Locust handbook (2nd. edn). London: ODNRI.
Venkatesh, M. V., Ahluwalia, P. J. S. & Harjai, S. C. 1972 Influence of rainfall on the egg diapause of *Oedaleus senegalensis* Krauss (Orthoptera, Acrididae). *Pl. Prot. Bull., New Delhi* **23**, 20–27.
Walsh, J. 1986 Grasshopper control program successful. *Science, Wash.* **234**, 815–816.

Discussion

N. D. Jago (*Overseas Development Natural Resources Institute, Chatham, U.K.*). The following comments reinforce the excellent paper by Dr Cheke. Two subject areas are of interest, the first biological, the second agro-economic and logistic and focuses on the estimated crop loss caused by *Oedaleus senegalensis* and other economically important Sahelian acridids.

ODNRI is well placed to comment because the Overseas Development Administration (ODA) has supported an ODNRI, farmer level, millet crop protection project in northwest

Mali since 1985. As leader of the programme, I have had a unique opportunity to observe fluctuations in grasshopper pest species during the period, starting with the massive outbreaks of *O. senegalensis* and *Kraussaria angulifera* (Krauss) in 1985 and 1986 and culminating in the truly remarkable and uniquely extensive outbreaks of no less than nine species in 1989. In rank order of pest status these were:

1. *Oedaleus senegalensis*, 2. *K. angulifera*, 3. *Hieroglyphus daganensis* (Krauss), 4. *Diabolocatantops axillaris* (Thunberg), 5. *Cataloipus cymbiferus*† (Krauss), 6. *Kraussella amabile*† (Krauss), 7. *Ornithacris cavroisi*† (Finot), 8. *Cryptocatantops haemorrhoidalis* (Krauss), and 9. *Aiolopus simulatrix*‡ (Walker).

Biological observations: migration

An example of conclusive evidence of northward movement occurred on 29–30 June 1986. Early and precocious rains between 22–27 May at latitude 13° 30′ N had caused hatching of *O. senegalensis* in an east-west belt of over 100000 ha, with hoppers at a density of 5 m^{-2}. These fledged some three weeks later. On 29–30 June a massive overnight arrival of young adults, associated with 37 mm of rain, took place at Madina Kagoro, a village at 14° 20′ N, just south of the project base at Mourdiah (14° 28′ N, 07° 28′ W), in an area which had hitherto received only light rain (7 mm). The fields showed some millet germination, but no previous hatching of *O. senegalensis*. The project mobilized a field survey and discovered an area of cultivated millet of some 200 ha covered with young adult insects, at an estimated density of 5 m^{-2}. Three days later, and before control could be mobilized, the insects disappeared during a night on which heavy rain fell. The Mourdiah region was once again empty.

The heavy rain led to wholesale hatching over the Mourdiah region. Eventually, intensive survey showed that 320 km^2 was occupied by hoppers, which formed marching bands and exhibited a tendency to grey-brown/black cuticular colour, in spite of verdent and abundant wild vegetation. Of the potential cultivated millet area, 25% was destroyed despite repeated attempts at replanting. Fledging took place at the end of July, and all the *O. senegalensis* left the Mourdiah area between 28 July and 30 August, leaving devastation behind them. From then till late September, areas south of 14° 50′ N were virtually free of the species.

Evidence for massive southward movement of *O. senegalensis* was obtained in September 1989. Between 5 August and 9 September, project areas south of latitude 15° 00′ N were completely overwhelmed by 6 major grasshopper pest species (see species 2–5 listed above). At this stage *O. senegalensis* was not included. After 11 September, north of 15° 00′ N, the fields and savanna were found to be filled with *O. senegalensis*, as fifth instar hoppers and young adults. By 14 September crop damage had started to accelerate and young adults were seen to be making local diurnal movements. On 19 September a massive influx of young adults occurred overnight at Nara (15° 10′ N, 07° 17′ W).

On 21 September a southward daylight displacement took place at a village 7 km west of Dilli (15° 00′ N, 07° 40′ W) (J. Legg, personal communication). The passage of flying adults took 1.5 h and started at 11h30. The movement took place on a front of at least 7 km, because it passed simultaneously through Dilli. At Mourdiah, 70 km further south and in the area devoid of the species since early August, young adults started coming to the light trap in small numbers during 17–18 September, numbers rising to gigantic proportions on the nights of

† Species that became major pests in Mali for the first time in 1989.
‡ Usually major pests in crops on heavy clay soils, hence of less importance to millet than to sorghum.

26–29 September and declining to 3 October. This set of observations represents evidence for a southward displacement of 70 km in about five days.

Observations on crop damage

Grasshoppers afford a much greater long-term and chronic menace to agriculture than do the classic locusts. The outbreaks of 1986 saw at least 2850 km^2 of the Nara area infested in mid-September with a mixture of *Kraussaria angulifera* and *Oedaleus senegalensis*. North of 15° 00′ N populations were almost exclusively *O. senegalensis*. Hoppers and adults formed densities of 90000–160000 ha^{-1} in the south, but *O. senegalensis* hoppers were commonly found at 170000–400000 ha^{-1} in the north. The scale of crop loss was probably on the same scale as that experienced in 1989, though over a smaller area. In addition, the USAID-sponsored aerial control came too late to protect northwestern Mali, though their helicopters were later able to tackle a part of an 800 km^2 area infested north of 15° 00′ N.

The crop loss incurred in the 10000 km^2 of infestations in northwestern Mali in August–October 1989 has been carefully studied by the ODA Project. This is the first time that a detailed assessment of crop loss due to grasshoppers has been made. Analysis of results is not yet complete, but a preliminary study shows that 5.7 % of the farmer population lost 70–90 % of their millet (mean loss 85 %) (C. Lock, personal communication). These losses occurred in the 13 worst-hit villages under study. In a separate study at Mamaribougou Ferribé (14° 56′ N, 07° 46′ W) by J. Legg (personal communication), results showed that farmers lost 24 % of the millet crop to grasshoppers. In the same fields the millet head miner *Heliocheilus albipunctella* Joannis caterpillar had fallen to very low levels compared with 1988, so that very little crop loss can be attributed to that pest. C. West (personal communication) estimates that the 280 pilot farmers over the region as a whole (latitudes 14° 00′ N to 15° 30′ N) lost 18 % of the millet to grasshoppers, confirming the impression that losses were greater toward the Mauritania border and north of latitude 15° 00′ N.

Concerning estimates of crop loss (see, for example, Walsh 1986), firstly, the area lost to agriculture because of early season attack is usually ignored. Secondly, harvest losses are more serious than they first appear because they are percentage losses on a harvest which, without grasshopper attack, is already inadequate for the needs of the family for one year. Thus, farmer families can be roughly divided into 90 % of small to medium size and poorer families (less than 29 members) and 10 % of richer, larger families (29 or more members). Lock *et al.* (1988, unpublished report) have shown that poorer families produce only 7.7 to 8.6 months supply in years of good rains, the equivalent for larger families being 11.2. I have calculated that taken overall, the harvest will be around 8.5 months supply without major grasshopper attack, but roughly 7.0 months supply when good rains are accompanied by massive losses generated by grasshoppers. This is on a scale which, if repeated for a number of years, could not be compensated for by the economic strategies currently open to the farmers. Last year (1988), for example, C. Lock (personal communication) discovered that 10 villages in the Dilli ‘arrondisement’ had incurred 70–95 % millet crop losses due principally to grasshoppers, with an estimated value to the average farm family of between 150000 and 200000 F.CFA (£300–£400). As a result, up to a quarter of families had left their village in search of millet and work elsewhere.

The value of crops lost interacts directly with the problem of the cost of the treatments available for grasshopper control. ODA, for example, is currently determined that any method of crop-yield improvement or crop-loss reduction should, as far as possible, pay for itself. The benefit: cost ratio could be greatly improved by avoiding waste. Pesticides are very expensive, yet for much of the time, when used against grasshoppers such as *O. senegalensis* attacking subsistence level agriculture, they are ineptly applied. Difficulties of aircraft navigation contribute to failure, even though the technology exists to avoid this, and personnel, including pilots, are often inexperienced. Electronic and other equipment needs to be made more suitable for field use in the tropics. This also applies to pesticide formulations for aerial and ground applications.

J. M. Ritchie (*Overseas Development Natural Resources Institute, Chatham, U.K.*). Dr Cheke has rightly drawn attention to the anecdotal nature of much of our information on the biology of *Oedaleus senegalensis*. By analogy to phase changes in locusts we accept that nymphal colouration changes do occur in *Oedaleus* in response to crowding. However, research is needed to clarify the effect of crowding on the biology of *Oedaleus* and, in particular, the conditions that cause band formation and the development of the characteristic brown and orange colour of 'gregarious' nymphs. Similarly, we know little of the degree of interaction between adults in dense populations and the extent to which their mobility and their fertility are affected by density as they are, for example, in the Desert Locust.

Further morphometric research is needed, employing multivariate techniques, to analyse a range of character measurements by using large samples from populations of known density, if we are to establish whether *O. senegalensis* merely shows allometry in certain characters in relation to overall size of the individual or whether, independent of size, there is a genuine separation into two distinct morphological phases, as in the major locust species.

Dr Cheke has emphasized that advance warning of potentially large nymphal populations at the start of the season can be provided by egg pod surveys. These surveys are greatly speeded up and improved by soliciting the observations of the farmers themselves on the extent and position of egg-laying by females towards the end of the previous rainy season.

Information from such surveys needs to be combined with new knowledge on the degree of hatching response of *Oedaleus* eggs to differing amounts of rainfall, building on the work of Dr Cheke and his colleagues. Improved coordination of rainfall data collection and processing in the Sahel would show likely areas for major concentration of egg hatching year by year. Early indications of rainfall can be obtained by the use of satellite imagery to detect changes in cloud temperature associated with precipitation and subsequent greenness resulting from the flush of new vegetation. Currently, ODNRI is planning to carry out further work on the inception and breaking of diapause in *Oedaleus*. The results of this study will then be combined with meteorological and egg-pod survey information to improve the forecasting of outbreaks.

The use of various pathogenic microorganisms to control *Oedaleus* has been touched on by Dr Cheke. The Commonwealth Agricultural Bureau International Institute of Biological Control is beginning a programme of research on pathogenic fungi, especially *Beauveria* and *Metarhizium*, which is targeted against the Desert Locust, but which might be equally applicable to *Oedaleus*. These pathogens are not released into the environment in the hope that they will become permanently established. Some strains are probably already present in areas occupied by the target insects. Instead, the aim would be to augment the natural level of infection by application of pathogens as biopesticides, sprayed onto the target as droplets in a carrier oil or mixed with baits. Pathogens therefore suffer from the same logistic problems of movement and storage as conventional pesticides, with the added problem of increased sensitivity to sunlight and high temperatures.

In *Oedaleus* most damage is done by final instar nymphs and young adults. The use of biocontrol will therefore require very precise monitoring of population build-up at the start of the rains so as to target young first-generation nymphs while they are still relatively immobile and before they cause damage. The delayed knock-down of pathogens compared with pesticides may make them initially unattractive to control personnel and farmers who are used to being able to verify the efficacy of treatment immediately.

L. D. C. Fishpool (*Overseas Development Natural Resources Institute*, *Chatham*, *U.K.*). I agree with Dr Cheke that existing models of the phenology of *Oedaleus senegalensis* populations fail to pay sufficient regard to the joint phenomena of egg quiescence and egg diapause. The picture of progressive northward displacements early in the wet season in response to the advancing rains, resulting in a more or less complete evacuation of the southerly source areas as the wet season advances, to be followed by complementary north to south return movements at the end of the rains, abandoning those opportunistically exploited more northerly latitudes as conditions cease to be favourable, is too simplistic. The implied quasi-total desertion by *O. senegalensis* of parts of its range at different times of the wet season is, I believe, more apparent than real. Significant populations of *O. senegalensis* eggs almost certainly occur throughout its range at all times of the year. While these populations may not be very large in relative terms, they are none the less important and need to be considered when attempting to interpret and describe the life cycle of *O. senegalensis*.

One consequence of them is that they call into question the concept of strategic control of *O. senegalensis*. Thus control of early season adult or nymphal populations in the south with a view to preventing or significantly reducing their subsequent recolonization of more northerly latitudes is unrealistic.

Given the vagaries of rainfall in the region in timing, amount and distribution, a life-cycle strategy involving an extended, but variable egg diapause by part of the population, makes sound evolutionary sense. It is almost literally a case of not putting all your eggs in one basket.

R. C. Rainey, F.R.S. (*Elmslea*, *Old Risborough Road*, *Stoke Mandeville*, *Bucks. U.K.*). Our own immediate interest in *O. senegalensis* is the evidence from detailed field observations of a direct effect of the Inter-tropical Convergence Zone on the distribution and structure of grasshopper concentrations. The evidence from radar offsets the absence of such observations on the Desert Locust from the Sahel region. During periods of massive grasshopper flights, the Airborne Radar (ABR) system might be a useful supplement to other monitoring methods.

P. Darling (*Agricultural Economist*, 46*a Ophir Road*, *Bournemouth*, *U.K.*). From what I have seen of semi-arid Africa, pastoralism is the most important means of economic livelihood; yet, in nearly all reports of locust and grasshopper damage (including this talk), the emphasis is firmly centred on damage to crops belonging to sedentary farmers. As far as I know, very little or no research has been done to assess the impact of grasshoppers on forage and browse. Some implications of this are that research on migratory pests is creating, confirming or conforming to the excessive attention paid by many national governments to the needs of cultivators at the expense of pastoralists. Surely, those conducting research on migratory pests should seriously consider expanding their terms of reference or work towards redressing this imbalance in some way? Spraying rangelands may be a more effective means of achieving control – it covers outbreak areas more thoroughly and it is easier to spray effective lines across extensive rangeland than limited cropland (though more widespread spraying may expedite the treadmill effect of strains becoming more resistant to sprays). Many past economic cost-benefit assessments of control measures in semi-arid areas must be totally inadequate for, by excluding the economic (and environmental) costs and benefits of control measures on pasturelands, they are often omitting the paramount form of economic (and environmental) activity in the areas being studied.

R. A. Cheke. There have been studies showing that over-grazing enhances grasshopper populations in the tropics (Merton 1959; Roffey 1970; Parihar 1981) and others with equivocal results (Amatobi *et al.* 1988) but, like Dr Darling, I know of no work devoted to the effects of grasshoppers or locusts on pastoralists in Africa. Such investigations would be difficult since a *sine qua non* of nomadic life is to migrate away from poor pastures, be they induced by insects or by drought. Nevertheless, I agree that studies would be worthwhile as both N. D. Jago (personal communication) and I have heard reports of grasshoppers destroying forage for cattle and camels. The extent of the depredations that grasshoppers inflict on grasslands, which we have both witnessed, must influence the well-being of shifting herds. Odiyo (1979) refers to a case where an infestation of armyworms (*Spodoptera exempta* (Walk.)) covering 65 km^{-2} of the Athi plains in Kenya, at a mean density of 28 sixth-instar larvae per square metre, were feeding at a rate equivalent to that of about 8000 cattle!

Regarding the spraying of rangelands, I urge caution as this might exacerbate grasshopper outbreaks by destroying too many of their natural enemies.

References

Amatobi, C. I., Apeji, S. A. & Oyidi, O. 1988 Effects of farming practices on populations of two grasshopper pests (*Kraussaria angulifera* Krauss and *Oedaleus senegalensis* (Krauss) (Orthoptera: Acrididae) in northern Nigeria. *Trop. Pest. Mgmt.* **34**, 173–179.

Merton, L. F. H. 1959 Studies in the ecology of the Moroccan Locust (*Dociostaurus macroccanus* Thunberg) in Cyprus. *Anti-Locust Bull.* **34**.

Odiyo, P. O. 1979 Forecasting infestations of a migrant pest: the African armyworm *Spodoptera exempta* (Walk.). *Phil. Trans. R. Soc. Lond.* B **287**, 403–413.

Parihar, D. R. 1981 Effects of over grazing on grasshopper population in the grasslands of Rajasthan desert. *Ann. Arid Zone* **20**, 291–294.

Roffey, J. 1970 *The effects of changing land use on locusts and grasshoppers* (ed. C. F. Hemming & T. H. C. Taylor), pp. 199–204. *Proc. Internat. Study Conf.* London: Centre for Overseas Pest Research.