

Ecology and management of the Senegalese grasshopper *Oedaleus senegalensis* (Krauss 1877) (Orthoptera: Acrididae) in West Africa: review and prospects

IDRISSA HALIDOU MAIGA⁽¹⁾, MICHEL LECOQ^{(2),*} & CHRISTIAAN KOOYMAN⁽³⁾

⁽¹⁾ Direction de la Protection des Végétaux BP. 323 Niamey, Niger

⁽²⁾ CIRAD Acridologie, TA A-50/D, F-34398 Montpellier cedex 5, France

⁽³⁾ IITA - Biological Control Centre for Africa, Cotonou, Bénin

* Corresponding author

Abstract. Following the droughts that occurred in the Sahel during the 1970s, the Senegalese grasshopper *Oedaleus senegalensis* (Krauss 1877) suddenly became the main pest grasshopper species in this region, where it regularly causes serious damage to crops, especially millet. The lifecycle of *O. senegalensis* reflects the precariousness of the Sahelian environment. The lifecycle and survival strategies of *O. senegalensis* have evolved to include migration following shifts in the intertropical convergence zone (ITCZ) and embryonic diapause in the dry season. It is thus able to cope with its natural hostile environment and remain in the most suitable ecological conditions for as long as possible. The alternation between outbreaks and recession periods seems to be related to the high spatiotemporal rainfall variability in the Sahel. Senegalese grasshopper outbreaks depend on the rainy season chronological pattern and on the initial quantity of diapaused eggs in the soil. Since the 1970s, many studies have been conducted on this species in the Sahel. Various models designed to monitor the population dynamics of this species have been published. However, some key factors that could explain the variability in outbreaks have not been seriously investigated. The present bibliographical review provides an overview on current knowledge while proposing some avenues for future research to enhance the sustainable management of this major Sahelian pest.

Résumé. Ecologie et contrôle du criquet sénégalais *Oedalus senegalensis* (Krauss 1877) (Orthoptera : Acrididae) en Afrique Occidentale : revue et perspectives. Depuis les années 1970, le criquet sénégalais - *Oedaleus senegalensis* (Krauss 1877) - est devenu l'un des principaux criquets ravageurs des cultures vivrières du Sahel africain. Il cause régulièrement des dégâts considérables, en particulier sur le mil. Le cycle biologique de ce criquet reflète la précarité de l'environnement sahélien. Cette espèce a développé un cycle biologique et une stratégie de survie incluant à la fois des migrations saisonnières suivant le déplacement du Front Intertropical (FIT) et une diapause embryonnaire pendant la saison sèche. Cela lui permet de faire face à un environnement souvent hostile et, pendant la saison des pluies, de se maintenir dans les conditions écologiques les plus favorables possibles. La succession de périodes de pullulations et d'accalmie est liée à la forte variabilité spatiale et temporelle de la pluviométrie et à l'abondance du stock d'œufs en diapause dans le sol en fin de saison sèche. Les nombreux travaux conduits au Sahel depuis les années 1970 ont permis une meilleure compréhension de l'écologie de cette espèce. Divers modèles ont été proposés pour suivre la dynamique de ses populations. Cependant, certains facteurs clés pouvant permettre d'expliquer les pullulations demeurent peu ou pas étudiés. La présente revue bibliographique fait le point sur les connaissances actuelles et propose des voies de recherche pour une gestion durable de ce ravageur.

Keywords: Senegalese grasshopper, ecology, pest management, migration, West Africa.

The Senegalese grasshopper, *Oedaleus senegalensis* (Krauss 1877) (Orthoptera: Acrididae), is one of the main acridian pests in Sahelo-Sudanian regions of West Africa because of the range of crops and wild plants it attacks and the extent of damage it causes. It is a grasshopper species, which are generally not very gregarious, contrary to locust species like the desert

locust, *Schistocerca gregaria* (Forskål), and migratory locust, *Locusta migratoria* (L.). In the Sahelian region of West Africa, the Senegalese grasshopper first had a major economic impact during the incredibly high widespread outbreaks that occurred in 1974, following a drought in the early 1970s. Serious damage to food crops was noted, especially millet (*Pennisetum* sp.). Until that time, few studies had focused on this species, so information on its habits was very sparse (Mallamaire 1948; Chopard 1950; Joyce 1952; Davey *et al.* 1959; Saraiva 1962; Bhatia & Ahluwalia 1967; Jago 1968; Batten 1969; Hergert 1975; Popov 1976). Since the

E-mail: maigidris@yahoo.fr, lecoq@cirad.fr, c.kooyman@cgiar.org

Accepté le 31 janvier 2008

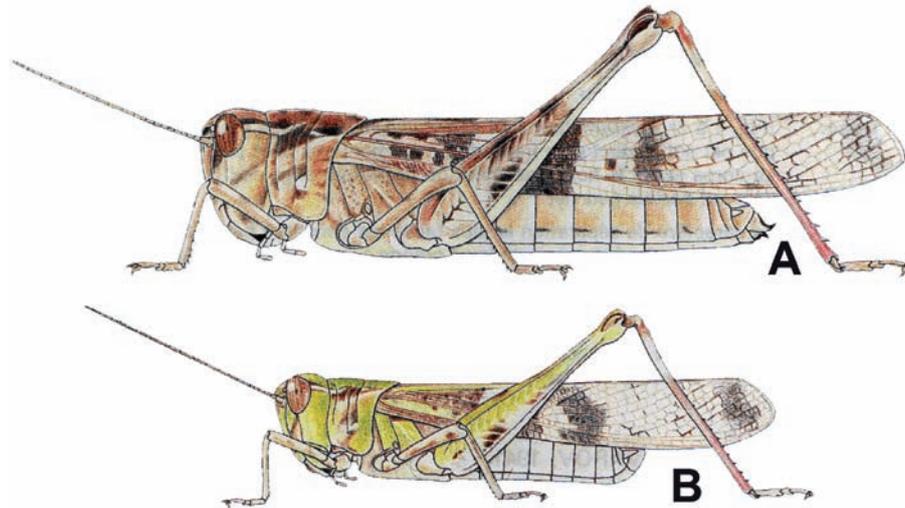


Figure 1
The Senegalese grasshopper: **A**, female; **B**, male. Drawings: J. Mestre 1988.

1970s, research has increased and more is known about this grasshopper species. Heavy chemical control treatments are still often necessary, despite the many studies that have been undertaken on the ecology of this insect, various attempts to model it for operational purposes and the advent of new biological pesticides.

An efficient environment-friendly control strategy has yet to be developed. The present bibliographical review summarises current knowledge on the Senegalese grasshopper, while proposing new avenues of research to enhance the sustainable management of this pest.

1. Natural history of the Senegalese grasshopper

Habitat and distribution range

Oedaleus senegalensis is a typical Sahelian grasshopper. Its distribution range covers the entire Indo-Saharan zone, from the Atlantic – including the Cape Verde archipelago – and extending as far east as central India. The species is especially abundant in tropical areas where it is classified as a pest regularly of substantial importance (COPR 1982). It has a low to nil economic impact elsewhere. In the West African Sahelian region, *O. senegalensis* colonizes annual grass communities dominated by Poaceae species such as *Cenchrus biflorus* Roxb, *Aristida mutabilis* Trin & Rupr., *Aristida adscensionis* L., *Eragrostis* spp., *Dactyloctenium aegyptium* (L.) Willd. and *Schoenefeldia gracilis* Kunth, along with a few woody and perennial species, especially *Aristida pallida* Steud, on sandy soils. It is distributed within an area where annual rainfall ranges from 200 to 1000 mm (Popov 1985, 1988). From north to south, there is a gradual shift from Sahelian rangelands – where the environment is suitable for grasshoppers for millions of hectares – to Sahelian croplands. In recent years, these croplands have gradually pushed

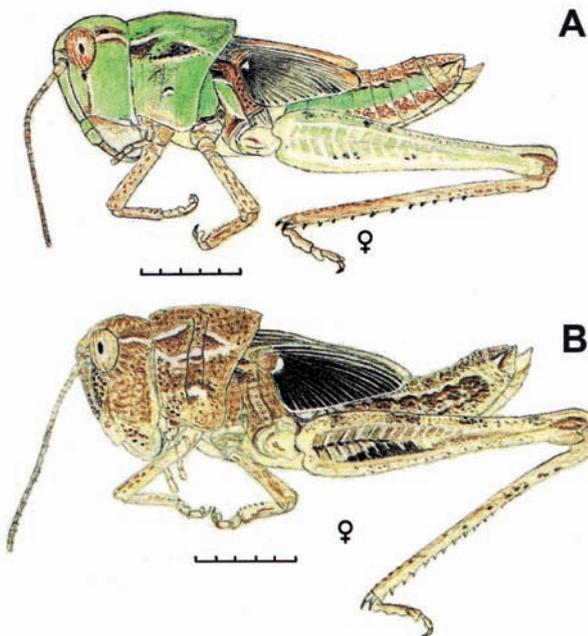


Figure 2
5th instar Senegalese grasshopper nymphs: **A**, green form and **B**, brown form with a gregarious tendency. Drawings: G. Popov 1989. (Scale: 1 cm)

northwards (into the traditional rangeland area), as a result of ever increasing population pressure, and also of soil depletion in the south. Conflicts between crop farmers and herders have thus worsened, with a concomitant increase in cereal crop damage caused by Senegalese grasshoppers (Batten 1969; Cheke *et al.* 1980; Popov 1985, 1988).

Description and morphology

The lifecycle and morphology of the Senegalese grasshopper have been described by various authors. These include Popov *et al.* (1990) for egg and egg-pod stages; Launois (1978a), Ritchie (1983), Launois & Launois-Luong (1989) and Popov (1989) for nymphal stages; and Mestre (1988), Lecoq (1988), Launois & Launois-Luong (1989) and Moizuddin (1991) for adults. For identification features and differences relative to similar species (especially *O. nigeriensis* hoppers, which are very similar to *O. senegalensis* hoppers), the best references are in Launois (1978ab), the revision of the *Oedaleus* genus by Ritchie (1981), Lecoq (1988), Mestre (1988), Launois & Launois-Luong (1989) and Launois-Luong & Lecoq (1989). The Senegalese grasshopper varies in colour from brown to green, apparently according to ecological and humidity conditions. Brown colouring is dominant at the onset and end of the rainy season, while green

prevails in the middle of the rainy season (Cheke *et al.*, 1980a; Chandra, 1983; Diop, 1987). On the Cape Verde islands, a form was described by Bolivar, in 1889, under the name *O. senegalensis* var. *dimidiatus*, which has darker pigmentation and its hindwings are black right to the base (Ritchie 1978; Duranton *et al.* 1983, 1984; Launois *et al.* 1988).

Life cycle

O. senegalensis generally has three generations (G1 to G3) a year during the rainy season and survives the form of diapaused eggs through the long dry season in the Sahel (Lecoq 1978a; Launois 1978b; Popov 1980; Cheke *et al.* 1980ab). The hypothesis of a fourth generation has been put forward when the rainy season is prolonged (Launois 1978b; Fishpool 1982), but there is no clear evidence of this phenomenon, which should thus be considered as exceptional (Popov 1988; Fishpool 1982). *O. senegalensis* is a graminivorous insect (Saraiva 1962; Ahluwalia *et al.* 1976; Launois-Luong 1980; Chandra 1982). Its dietary range reflects the relative abundance of wild grasses in the field (Boys 1978). The results of studies of Dahdouh *et al.* (1978), Duranton & Lecoq (1980), Lecoq (1984) indicated that it is a mesoxerophilous species with a geophilous tendency in the rainy season, and it is widely distributed in fallow and crop fields and in the natural environment.

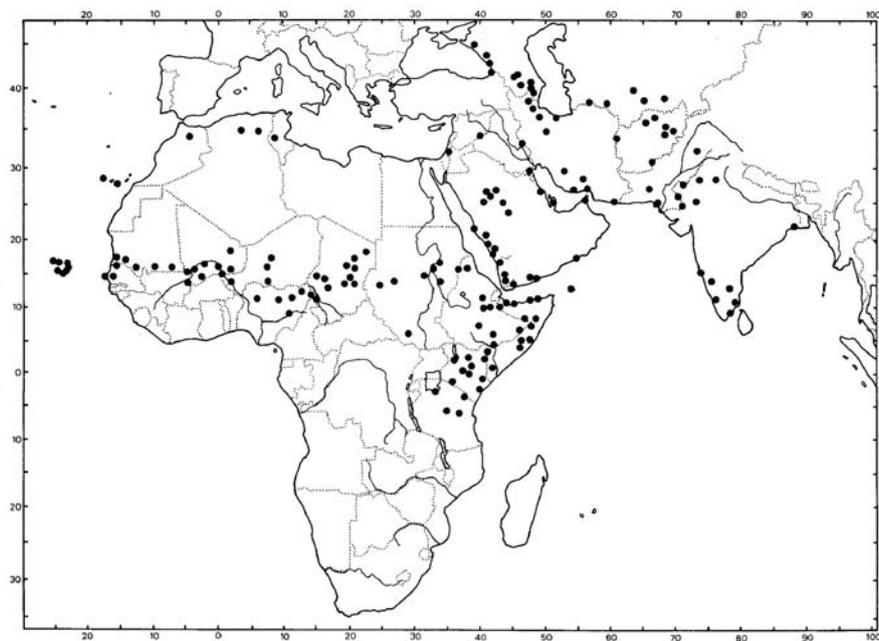


Figure 3
Senegalese grasshopper distribution range (from Ritchie 1981).

Under suitable conditions and without diapause, the lifecycle of this species lasts less than 2 months (Fishpool 1982; Popov 1988). The mean embryonic incubation period is 2 weeks: 8–10 days (Cape Verde, Saraiva 1962), 12–15 days (Mali, Castel 1975 *in lit.*), 15 days (Sahel, Launois 1978b), 12–15 days (Sahel, Popov 1988), 10–11 days (Sahel, Fishpool 1982), and it varies according to the soil temperature (Diop 1997). The following times have been reported for hopper development: 3 weeks (Mali, Davey *et al.* 1959; Cape Verde, Saraiva 1962), 24 days (India, Bhatia & Ahluwalia 1967), 22 days (Sahel, Launois 1978b), 16–20 days (for males and females, respectively, in Mali, Castel 1975 *in lit.*), 17–20 days (Popov 1988) and 15 days (Sahel, Fishpool 1982). For each instar (between 31 and 38 °C), Bhatia & Ahluwalia (1967) reported times of 6, 7, 4, 4 and 2 days for instars 1 to 5, respectively (but the 2-day duration for the 5th instar is surprisingly short). Launois (1978b) noted durations of 4, 3, 5, 5 and 5 days, respectively. Ovocyte maturation lasts 2 weeks on average: 8–15 days (Cape Verde, Saraiva 1962), 10 days (Sahel, Launois 1978b), 10 days (Sahel, Fishpool 1982) and 15 days (Sahel, Popov 1988, Launois & Launois-Luong 1989, Launois-Luong & Lecoq 1989). The mean number of ovarioles per female ranges from 37 to 43 (Launois-Luong 1979a; Chiffaud & Mestre 1991); and females lay eggs once or twice, with each egg laying period lasting 5–6 days (Launois-Luong 1979ab).

Eggs are preferentially laid in humid sandy or sandy-loamy soils. Various studies have focused on females' choices of egg laying sites and on embryonic development (Bhatia & Ahluwalia 1967; Venkatesh *et al.* 1972; Popov 1980, 1987; Amatobi 1985; Diop 1995). Egg laying may be noted during the day (Cheke *et al.* 1980b; Chandra 1983) but mainly occurs at night (Popov 1980). Egg-pod densities are sometimes very high, e.g. 8–37/m² (Cheke *et al.* 1980b, in Niger), 31/m² (Saraiva 1962, in Cape Verde), 12–15/m² (Popov 1980, southwestern Niger), or much lower, e.g. 0.1–0.5/m² (Launois-Luong 1979a, southern Niger, Maradi) and 2.34/m² (Cheke *et al.* 1980b, SW of Niamey in Niger).

Eggs laid by the first two generations (G1 and G2) develop continuously. At the end of the rainy season, eggs laid by the last generation (G3) enter diapause, spend the dry season in the soil before hatching at the onset of the following rainy season (Joyce 1952; Davey *et al.* 1959; Saraiva 1962; Venkatesh *et al.* 1972; Lecoq 1978a; Popov 1980; Diop 1987; Moizuddin 1991; Gehrken & Doumbia 1996). After mid-September, most *O. senegalensis* eggs laid do not hatch within a normal period, even if the soil is humid (Launois

1978b; Popov 1980). The photoperiod is the factor that determines whether or not diapaused eggs are produced. Diapause is induced by short photoperiods (12 D:12 N) under cool temperature conditions (25 °C) (Diop 1993; Colvin & Cooter 1995). Non-diapaused eggs are mainly produced (97%) under high temperature (40 °C) and long photoperiod (14 D:10 N) conditions (Colvin & Cooter 1995; Diop 1995). Eggs reach the anatrepsis stage (in which they remain until development resumes) in 12–15 days in dry soils and in just 3–5 days in humid soils (Gehrken & Doumbia 1996).

Diapause lasts 7–8 months and the eggs then remain in quiescence until the humidity conditions become suitable. Moisture is necessary to trigger development (Gehrken & Doumbia 1996). At the onset of the rainy season, the first hatchings are induced by the first rainfall of over about 20 mm. These perfectly coincide with the emergence of the first cereal crops which the hoppers are likely to feed on and seriously damage, thus forcing farmers to sow their crops several times in a row (Popov 1980; Diop 1987; Venkatesh *et al.* 1972). Lighter rainfall just induces partial hatching and the unhatched eggs remain in quiescence or start developing to hatch at the next rainfall. The first instar hoppers derived from post-diapause hatchings appear at least 3–13 days after the eggs are first moistened (Castel 1975 *in lit.*; McAleer 1977; Launois 1978b; Popov 1980; Cheke *et al.* 1980a; Fishpool 1982; Amatobi 1985; Diop 1987). Some eggs, however, do not develop at the onset of the rainy season, even after they have been moistened. Egg hatching is more or less temporally staggered. This mechanism likely ensures survival when there are localised rains followed by long dry periods (Cheke *et al.* 1980a; Launois *et al.* 1996).

There have been regular reports on diapaused eggs surviving for several years when environmental conditions are unsuitable (Saraiva 1962; Venkatesh *et al.* 1972; Cheke *et al.* 1980a; Fishpool & Cheke 1983; Popov 1980, 1996). This phenomenon has been mentioned as a possible cause of massive outbreaks of this species. F.V. Barbosa (in Saraiva 1962) thus reported serious outbreaks on Boa Vista island, Cape Verde, in 1948 after 5 years of drought during which this species was completely absent. The eggs had thus remained in the soil for 5 years without substantial mortality. This finding was, however, just based on interviews with local inhabitants, not on reliable data. It is even impossible to know whether the 1948 outbreaks were actually autochthonal or the result of massive arrivals of *O. senegalensis* from the continent – but nocturnal migrations of this species were unknown at the time. We consider that this phenomenon concerns just

a very slight proportion of the population in the natural environment (where there is generally high egg mortality due to natural predators) and must have very little real impact on the population dynamics. Colvin (1996), in the field, find only 1.4% of eggs remaining in diapause after a single dry season. The outbreaks could undoubtedly be explained by other factors, particularly by a series of suitable conditions during the rainy season, possibly following a dry period which would reduce the impact of natural enemies.

Behaviour

The behaviour of Senegalese grasshoppers – general activities, feeding, local movements, sexual displays, mating and egg laying – has been described by various authors, including Bhatia & Ahluwalia (1967), Ahluwalia *et al.* (1976), Chandra (1982, 1983) and Amatobi *et al.* (1991).

The species' group behaviour is clearly the most interesting aspect. At high densities, Senegalese grasshoppers show incipient gregarious behaviour, with a clear tendency to form hopper bands and swarms. This gregarious behaviour has been reported several times, with respect to hopper instars, by Joyce (1952), Saraiva (1962), Bhatia & Ahluwalia (1967), Descamps (1953), Batten (1969) and Popov (1988). Band fronts can be as long as 50–200 m, and even up to several kilometres. Joyce (1952) claimed that in several areas these bands resembled locust formations, but their densities were much lower (only 2–5 hoppers per m² according to Joyce, whereas locusts may be observed at densities of several hundreds or even thousands of individuals per square metre).

“Swarms” have also sometimes been described. These, however, seemed to just be clusters of high numbers of individuals in cases of high outbreaks, rather than actual swarms with gregarious behaviour as noted in locusts. *O. senegalensis* swarms do not display coordinated gregarious behaviour like locusts, nor do they undergo massive diurnal movements, sometimes at high altitude and covering long distances of tens to hundreds of kilometres a day. These Senegalese grasshopper “swarms” fly mainly at night, like isolated locusts (Riley & Reynolds 1983; Ahluwalia *et al.* 1976). Diurnal flights are generally more discrete and generally at altitudes of just 2–3 m. These flights are intermittent and cover very short distances of 1 km/day at most (Bhatia *et al.* 1962, 1967; Ahluwalia *et al.* 1976; Popov 1976).

In Senegalese grasshoppers, no studies have highlighted morphometric variations associated with population densities as high as those noted in locusts (Bhatia & Ahluwalia 1967; Ahluwalia *et al.* 1976;

Cheke *et al.* 1980a; Chandra 1983; Moizuddin 1991). Studies of Ritchie (1981) on potential morphometric changes associated with a phasal effect gave negative results. Only hopper coloration varies, i.e. hoppers in high density bands have a darker pigmentation than isolated individuals (Popov, 1989, especially noted a darkening around wing buds and the outer side of the hind femurs). Contradictory results have also been reported, suggesting that there is an incipient phase polymorphism phenomenon in this species (Bindra *in* Popov 1988), but this would have to be confirmed in controlled conditions.

Mortality factors and natural enemies

The most known causes of natural mortality are those that affect embryonic development (Greathead 1963; Cheke *et al.* 1980b; Popov 1980).

Eggs laid are not all viable, but the relatively constant percentage of sterile eggs does not surpass 10% (Colvin 1997). Otherwise, there can be very high destruction by biological agents (parasitoids and predators) or natural factors (excessive drought or humidity). In the Sahel, Popov (1980) showed that mortality caused by natural enemies can sometimes be as high as 50–80%. However, there is very high and yet unexplained regional and temporal variability.

Predators and parasitoids are commonly noted on eggs of Senegalese grasshoppers and all other acridians. In a sample of 1 340 egg pods collected in Niger, Popov (1980) showed that parasite-induced mortality in *O. senegalensis* eggs was 58% overall, including 40% by *Pimelia senegalensis* (tenebrionid), 11% by *Systoechus* (bombylid), 4% by *Xeramoeba oophaga* (bombylid) and 3% by *Mylabris vicinalis* (meloid). If an egg pod is partially attacked, undamaged eggs end up drying out and dying. Popov (l.c.) only noted a minor impact of scelionids, whereas even in Australia *Scelio fulgidus* Crawford can cause high mortality (> 90%) in *Chortoicetes terminifera* eggs in declining populations (Farrow 1977). This low hymenopteran parasitism rate in Senegalese grasshoppers was confirmed by Van der Weel (1989 *in lit.*) who, during egg pod surveys in Niger in 1988 and 1989, recorded only one case at over 440 sites where several thousands of *O. senegalensis* egg pods had been collected.

However, in a study carried out at Banizoumbou, western Niger, on 860 grasshopper egg pods (species not specified), Garba (1998) noted a relatively high rate of scelionid parasitism (16% in the rainy season, 9% in the dry season). For other Sahelian acridian species, Shah *et al.* (1998) also noted rates of scelionid (*Scelio africanus* Risbec and *S. mauritanicus* Risbec) egg pod parasitism rates as high as 3.3%. Moreover, Garba (l.c.)

found that meloids were responsible for 9% mortality during the rainy season and 5% in the dry season. Cheke *et al.* (1980b), found that only 25% of 142 egg pods collected at the end of the egg-laying period had been damaged by parasites, i.e. 13% by *Systoechus* sp. and 11% by other predators, including tenebrionid, histrid and meloid larvae. This parasitism rate increases as the dry season progresses, and Yonli (1990) thus found that the parasitism rate gradually increased from 39% in December (onset of the dry season) to 60% in April (end of the dry season). The regular egg pod surveys carried out in recent years by crop protection services in Niger have confirmed the high impact of natural enemies on Senegalese grasshopper diapaused eggs, and a parasitism rate of sometimes around 100%, but rates vary markedly between regions and years (Niger Crop Protection Service, *pers. com.*).

Senegalese grasshopper nymphs and adults may also be preyed upon by parasitoid insects, mites, nematodes and many vertebrate and invertebrate predators (Bhatia & Ahluwalia 1967; Ahluwalia *et al.* 1976; Cheke *et al.* 1980a; Popov 1988; Amené & Vajime 1990). Amené & Vajime (1990), over a 3-year monitoring period, obtained a predation rate of 5.6% due to parasitoid insects, including: *Trichopsidea costata* (3.9%); *Blaesoxipha filipjevi* (1%) and *Sarcophaga scheomani* (0.7%). Parasitism by a mite, *Eutrombidium*, has also been reported in nymphs (30.2%) and adults (21.1%). There are many arthropod predators, including spiders (*Argiope* sp.), scorpions, Asilidae (*Promachus* spp.), mantids (*Empusa fasciata* Sauss. and *Sphodromantis lineola* L.) (Amené & Vajime 1990). Various vertebrates also feed on Senegalese grasshopper nymphs and adults. Amené & Vajime (1990) noted a lizard (*Agama agama* L.), three snakes (*Psammophis sibilans* Fisher, *Mehelya crossii* Schlegel and *Rhamphiophis oxyrhynchus* Schlegel), and various birds: *Lanius excubitor* L., *Merops nubicus* Gmelin, *Merops albicollis* Vieillot, *Corvus albus* Müller; *Ardeola* (= *Bubulcus*) *ibis* L., *Ciconia abdimii* Lichtenstein, *Buteo augularis* Salvadori. Henry *et al.* (1985) reported microorganisms that are pathogenic to West African grasshoppers like *O. senegalensis*: a virus (*Entomopox*, affecting *Oedaleus*), Amoebidae protozoans (*Malamoeba locustae*), Eugregarinidae and two Microsporidae. Diop (1997) reported isolating a fungus, i.e. *Metarhizium anisopliae*, on dead *O. senegalensis* individuals collected in August 1994 in Niger (around 11% of individuals contaminated).

Various general studies on acridians have highlighted the beneficial impact of natural enemies on diminishing outbreaks, even though it is generally known that they could not actually stop outbreaks (Greathead 1963, 1992). However, the impact of natural enemies varies

substantially between regions and years even though the reasons underlying this variation are not yet known.

The impact of these enemies should be determined even though they may not actually be able to stop an upsurge when ecological conditions are highly suitable for grasshoppers, especially considering that some hypotheses put forward to explain serious outbreaks (e.g. in 1974) refer to the reduction of the impact of natural enemies after exceptionally long dry periods (Colvin & Holt, 1996; Holt & Colvin, 1997). The role of egg predators is a very important point to clarify, especially with respect to diapaused eggs, which are highly exposed to natural enemies during several months of the dry season. In addition, these natural enemies are not specific to Senegalese grasshoppers, they affect acridians overall. Studies to gain insight into their role should thus be focused on acridian populations in general, not just on one individual species. Finally, it is hard to gain insight into the roles of these natural enemies due to the serious lack of accurate information on their biology and ecology.

Migration

Recent studies have shown that Senegalese grasshoppers, like many acridian species in West African Sudanian and Sahelian areas, can fly very long distances carried by the winds at night. These movements represent a form of seasonal migration between successively suitable breeding areas. Increasing evidence has been reported over the last 30 years that Senegalese grasshoppers and many Sahelian locust species undertake long-range nocturnal migration flights (Reynolds & Riley 1988; Riley & Reynolds 1979, 1983, 1990).

Regionally, these movements are linked with environmental instability and seasonal rainfall variations, which in turn are associated with shifts in the intertropical convergence front (ICF). The northward shift in the ICF at the onset of the rainy season leads to a gradual increase in biotope hygrotrophy. Many species are thus obliged to move as the momentarily suitable environment gradually becomes too humid. Southwesterly air currents carry these insects (G1 and G2) to more northern regions where there is less rainfall and ecological conditions are more suitable. This general movement of the acridian fauna thus gradually accompanies the slow northward shift in the ICF. This phenomenon is reversed at the end of the rainy season. Acridians (generally G3) are gradually forced out of these regions as the biotopes dry out and are drained by northerly winds, and they accompany the ICF in its rapid southward retreat (Launois 1978b; Lecoq 1978ac, 1995).

These seasonal movements – whose conditions vary according to the species, lifecycle and ecological niche – are observed in may acridians, as in many other insects (cf. studies of Duviard, 1973, on seasonal migrations of the cotton bug *Dysdercus völkerei* Schmidt in relation with ICF movement patterns in West Africa), including *O. senegalensis* (Lecoq 1978ac).

Various data confirm these movements, in addition to direct radar observations. In Sudan, Schaeffer (1976) thus documented migrations of the locust *Aiolopus simulatrix*, while Riley & Reynolds (1979, 1983) and Reynolds & Riley (1988) recorded several migrations of *O. senegalensis*. Field counts of population numbers (Golding 1934; Joyce 1952; Lecoq 1978ac; Duranton *et al.* 1979; Popov 1976, 1988) revealed certain population structures that could only be explained by seasonal migration phenomena. Offshore captures, far from any coasts, revealed that this grasshopper has the endurance necessary to undertake such long-range migration flights. Ritchie (1978) reported capturing Senegalese grasshoppers offshore in the Atlantic, 160 km from the West African coast. Finally, light-trap captures have also provided evidence of these movements (Lecoq 1978ac). *O. senegalensis* adults are highly attracted by light (Launois 1978b; Jago 1983; Fishpool 1982; Diop 1987), mainly during nights when there is very little moonlight (Jago 1983; Diop 1987). Such light captures are generally considered to be evidence of nocturnal seasonal migrations. L.D.C. Fishpool (in Reynolds & Riley 1988) showed that an increase in nocturnal Senegalese grasshopper activity and an increase in light-trap captures were associated with unsettled weather, such as the passage of a squall line. Lecoq (1978a), in a study lasting more than 2 years involving two light traps and terrestrial population studies, showed that the density of light-trap captures was directly related with long-range seasonal acridian (including Senegalese grasshopper) movements. These captures were maximal when the ICF was in the vicinity of the trap, i.e. around 100 km northward. Capture densities increased regularly as the ICF shifted northward, and decreased as it moved further away. Densities increased again when the ICF shifted southward again at the end of the rainy season. However, a comparison with radar data recorded by Reynolds & Riley (1988) showed that the density of flying grasshoppers was not very correlated with the number of locusts captured in light traps. Farrow (1979) showed that these light traps mainly captured immigrant individuals, whereas few emigrants and individuals transiting at high altitude were captured.

Grasshoppers often fly in the same direction, i.e. in the direction of the wind when it is strong, and their flying speed is boosted by the wind speed. Their

orientation sometimes differs, but the angle relative to the wind direction is always less than 90° and they never fly against the wind. Different orientations may be noted under low wind conditions. They may take short-range flights that are not directly related to the wind direction. These movements enable the species to explore its habitat within a limited geographical area (Reynolds & Riley 1988; Riley & Reynolds 1979, 1983, 1986, 1990).

Southward Senegalese grasshopper movements at the end of the rainy season are better documented, e.g. by Popov (1976), Lecoq (1978ac), Cheke *et al.* (1980a) and Amatobi *et al.* (1991). These are generally quick massive movements. At this period, swarms of Senegalese grasshoppers may from one day to the next invade crop fields and destroy them within a few hours. These movements have been especially well illustrated by radar recordings – a technique that is useful for monitoring the movements of flying insects – thus highlighting that they can move between areas, carried by the wind, accompanied by other acridians and insect species (Riley & Reynolds 1979, 1983, 1990). These nocturnal southward flights after the end of the rainy season (early November) were first documented in the central Niger River delta region in Mali (Riley & Reynolds 1983). Later they were recorded during the night of 21–22 October 1978, when a high concentration of grasshoppers was detected by radar in Tilemsi Valley in Mali, and then 2 h later they were detected passing over another radar station 100 km further south. *O. senegalensis* likely accounted for most of this flying population (associated with *Diabolocantops axillaris* Thunberg, *Acrotylus longipes* Charpentier, *Aiolopus simulatrix* Walker, *Ochrilidia* spp.). This flight is direct and spectacular evidence of a southward migration of Senegalese grasshoppers at the end of the rainy season, carried by northeasterly and northerly winds accompanying the southward retreat of the ICF (Riley & Reynolds 1983). The wind conditions mainly determined the flight altitude and direction. Insects in flight, probably immature, were mainly flying in the wind direction, between 145 and 440 m altitude, at a mean speed of around 15 m/s. It has been estimated that, when carried by the wind, these grasshoppers could frequently fly distances of at least 50 km per night, and there are even reports of 350 km migrations on some nights (Riley & Reynolds 1979, 1983). Northward movements at the onset of the rainy season are more discrete, progressive and less documented. There have just been a few reports in Burkina Faso by Lecoq (1978ac), and in Mali by Reynolds & Riley (1988), Popov (1988) and Jago (in Diop 1997).

Due to these flights, successive generations of Senegalese grasshoppers occur in different areas. This explains the often contradictory observations of various authors in the past. Golding (1948) reported observing just one generation in Nigeria, like Joyce (1952) in Sudan. Two generations were observed by Davey *et al.* (1959) in Mali and by Descamps (1975) in the Chad Lake basin. Saraiva (1962) noted that the number of generations in Cape Verde depended on the rainfall levels and varied from one to two depending on the year, but the species was sometimes completely absent. Fishpool (1982) reported four generations at the same site during an exceptionally rainy year. Launois (1978b) and Lecoq (1978a) showed that, within a distribution range, the mean number of yearly generations seemed to be three, but that the number of successive generations at the same site depended on the location within this seasonal north-south migration system. A single generation was then observed at the northern extremity, with three generations of unequal size at the southern extremity and two generations in the intermediate zones. However, large-scale and almost constant migrations were noted between these different areas, so the local population dynamics were often very complex. At a given site, the number of generations present is difficult to accurately determine, as there is a constant mixture of individuals of different

generations. The overall patterns of these north-south migrations vary markedly according to between-year variations in meteorological conditions, especially the rainfall and wind regime (Bhatia & Ahluwalia 1967; Launois 1978b; Diop 1987).

For the Senegalese grasshopper, these long-range migrations are an adaptation to the fragmented and temporary aspect of suitable habitats in semiarid Sahelian and Sudanian areas where the spatial and temporal rainfall distribution is shifting and erratic, especially at the beginning and end of the rainy season (Launois 1978b; Lecoq 1978ac; Reynolds & Riley 1988). This enables these grasshoppers to benefit maximally from their environment. During the rainy season, they can thus move into new habitats as they become suitable, while the production of diapaused eggs at the end of the rainy season enables the species to overcome the drastic conditions during the dry period that lasts several months (5–6) in the Sahel (Popov 1980; Cheke *et al.* 1980 ab). Risks associated with migration and colonization of new suitable habitats seems to be generally lower than that inherent to remaining in the same habitat (Southwood 1977; Dingle 1980). In addition, it seems that losses during insect migrations are generally lower than previously assumed (Rankin 1985) and that various orientation mechanisms of airborne migrants can substantially reduce mortality during migration (Farrow *in* Hughes 1979).

Migrations likely also enable Senegalese grasshoppers to avoid their natural enemies and disease threats. In addition, they can find more suitable food and produce more eggs by migrating southward at the onset of the dry season. Finally, Cheke *et al.* (1980a) pointed out that another advantage of this southward migration is that embryonic development of eggs laid in southern areas occurs earlier as a result of an earlier onset of the rainy season in the south, so the reproduction rate is consequently higher.

This utilization of nocturnal synoptic wind systems for long-range migrations is common to many acridians (Riley & Reynolds 1979, 1983, 1990; Schaefer 1976; Rainey 1976, 1979). It is known that such downwind flights are an efficient behavioural strategy, as already shown in desert locusts, especially for finding breeding sites. Grasshoppers thus tend to be carried to low elevation convergence zones (commonly the intertropical convergence zone, ITCZ) where the rainfall probability is highest (Rainey 1951, 1963, 1976). Grasshoppers carried by the winds are thus inevitably concentrated in convergence zones (Rainey 1976; Pedgley 1980), thus boosting their destructive potential (as discussed later).

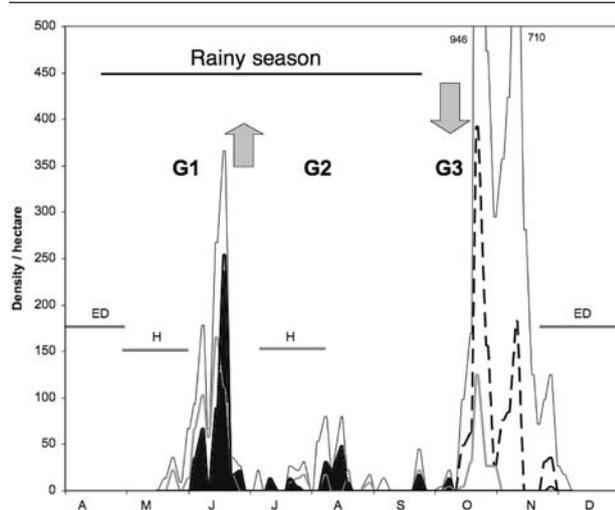


Figure 4 Life cycle of the Senegalese grasshopper in the first breeding area within the Sudanian zone in Burkina Faso (modified from Lecoq 1978a). **G1, G2, G3:** successive generations. **ED,** embryonic diapause. **H,** period when hoppers are present. Solid line: overall density of adults; dark area: density of soft-regumented fledgelings; shaded line: density of hard-regumented immature females; dashed line: density of females that have laid eggs. Arrows indicate the main migration phenomena; departures (upward arrow) and arrivals (downward arrow).

Finally, this Sahelian environment – with fragmentary habitats resulting from the high spatial and temporal rainfall variability – has shaped the survival strategy of this species, which is based especially on its migratory behaviour (Dingle 1986; Taylor 1986). This is associated with the development of embryonic diapause in response to the deterioration of this habitat during the long arid Sahelian dry season. These movements are such that at a given site two almost equally important factors determine the grasshopper population density, i.e. local reproduction and long-range migrations, which are responsible for a very rapidly changing grasshopper arrival-departure pattern (Lecoq 1978a, 1995). All attempts to model Senegalese grasshopper population dynamics should account for these two key factors.

Modelling the population dynamics

Various Senegalese grasshopper population dynamics models have been developed to explain and forecast outbreaks, but none of them are currently fully operational.

The Launois model (1978b)

Over the last 30 years, there have been various attempts to model Senegalese grasshopper population dynamics. In 1978, Launois was the first to propose an empirical ecological model to monitor migrations and predict outbreak risk areas. According to this author, and on the basis of field observations of seasonal distributions, lifecycles and migrations, Senegalese grasshopper populations tend to concentrate and multiply in areas with a monthly rainfall level of 25–50 mm. This is considered to be the optimal rainfall level for the survival and reproduction of this species. On this basis, Launois (1978b) subdivided the distribution range in the Sahel, between 10° and 18° latitude N, in three areas that seemed to have complementary roles and between which the Senegalese grasshopper migrates on a seasonal basis, thus successively colonizing and utilizing these three areas. From south to north, there is the first breeding area (FBA), with 750–1000 mm annual rainfall, followed by the intermediate breeding area (IBA), with 500–750 mm, and the northern breeding area (NBA), with 250–500 mm (Launois 1978b, 1979; Arnaud *et al.* 1982; Lecoq 1995). This has become a standard and widely used classification, even though the nature and extent of population exchanges between these three areas and their respective roles in the population dynamics of this grasshopper need to be specified. The geographical locations of these areas are not fixed, i.e. their boundaries vary from year to year according to the rainfall distribution. Finally, east-

west migrations certainly take place and the extent of these phenomena would warrant assessment.

Also according to Launois (1978b), the three annual generations of Senegalese grasshoppers successively arise in each of these areas between which the grasshoppers migrate seasonally. Schematically, the first generation (G1) hatches at the onset of the rainy season in the southern part of the range (FBA). As temperatures rise and with the onset of the first rains, diapaused eggs laid by G3 (from the rainy season of the previous year) begin developing, giving rise to G1 hoppers and adults. In cropping areas, G1 hatching coincides with the emergence and germination of the cereal crop. In outbreak years, nymphs can destroy millet and sorghum crops, so farmers are forced to resow them several times. When FBA becomes too humid, G1 fledglings migrate (excessive humidity), leaving Sahelian croplands to colonize rangelands, thus giving rise to the third generation (G3) in NBA. In this area, competition between grasshoppers and livestock for rangeland resources is inevitable, but still poorly evaluated. As mentioned above, all of these migration movements coincide with the northward shift in the monsoon front and the gradual increase in rainfall. They are favoured by the southwesterly monsoon winds.

At the end of the rainy season, G3 adults arise just as the environment is beginning to dry out, so they are forced to leave. They migrate, following the intertropical front as it shifts southwards. Depending on the rate at which the intertropical front shifts, some gravid females will lay their eggs in NBA or IBA but, according to Launois (1978b), most ovipositions take place in FBA. When there is an extended rainy season and the intertropical front is delayed in a more northern position than normal, *O. senegalensis* could lay eggs at the end of the rainy season at more northern latitudes (NBA, IBA) than in normal years. As of September, the G3 eggs laid are in diapause and pass through the dry season to hatch only during the following rainy season.

Popov (1980), in a study on the regional distribution of Senegalese grasshopper egg pods at the end of the rainy season in western Niger and southeastern Mali, actually documented a gradual increase in egg-pod densities over a descending latitudinal gradient. These densities were low north of the 15th parallel, higher between the 15th and 14th parallel, with a peak between the 14th and 13th parallel, followed by a rapid decrease further south. Generally, the increase in egg-pod densities from north to south is gradual and seems to be associated with the progressive maturation of females during their southward movement.

Yearly variations in rainfall features are responsible for variations in migration ranges, within the preceding overall scheme. These features generally explain the different degrees of success of each generation, and the outbreak and crop damage potential. The relatively high synchrony between spatiotemporal changes in suitable areas and the phenology of acridian populations (and their capacity to fly) is a key feature.

Temporal and spatial monitoring of these suitable areas, as defined by Launois (1978b), is thus essential for crop protection. A Senegalese grasshopper population dynamics and migration monitoring model (OSE model) was developed by Launois (1978b, 1979, 1984), which takes most key factors into account, including rainfall, day length, air temperature and soil water balance. This model was designed on a Senegalese grasshopper distribution range scale and functions on a 10-day time step. It simulates, amongst other parameters, the phenology of grasshopper populations (but not their density) and generates maps of areas suitable for this species to develop. By interpreting the maps, variations in areas where there is a high risk of outbreaks can be monitored. These are areas where immigrant populations tend to group and breed with high success. It is thus possible to locate massive hatching areas at the onset of the rainy season, i.e. where there

is a much higher cereal crop damage risk. South-north grasshopper population movements can be monitored during the rainy season. The southward migration of G3 populations is especially important to monitor. These populations develop in the Sahelian rangelands and are often very dense. They migrate massively as swarms at night and can cause major damage when they settle in cereal crop fields. At the end of the rainy season, the model can be used to try to locate areas in which G3 eggs are concentrated – hoppers that subsequently hatch could potentially threaten crops at the onset of the following rainy season.

In 1990, this model was used by different crop protection services in Sahelian countries as a decision support tool for field operations, to guide surveys in risk areas, and to indicate where to position grasshopper control equipment (Launois & Lecoq 1990). However, several problems became apparent under these operational conditions, especially concerning the shortage of rainfall data. In addition, it seems that this complex and not very user-friendly tool was maybe too hastily transferred to crop protection services.

Remote sensing and vegetation indices

To overcome the shortage of field data, various studies have focused on monitoring biotope change dynamics for the purposes of early detection of areas where ecological conditions are suitable for grasshoppers. These studies are based on the use of NOAA/AVHRR low resolution satellite data but with high replication. Hielkema (1991), Hielkema *et al.* (1981, 1986) and Tucker *et al.* (1985) showed that remote sensing could be used to evaluate ecological conditions prevailing in desert locust breeding areas. The principle is based on the detection of significant green areas in a desert unit that could be suitable for the development of this insect. The low resolution of NOAA data used has long been a drawback in areas with low plant cover and where biotopes suitable for desert locusts are often relatively small. Recent developments show that it is possible to obtain an operational tool for real-time detection and monitoring of suitable biotopes. FAO and its acridian group now regularly use NOAA, SPOT4/VEGETATION and MODIS satellite data to assess ecological conditions in desert locust distribution ranges, especially rainfall and green vegetation growth. The products developed are constantly being upgraded and used to help national survey teams in detecting potential desert locust breeding areas (FAO 2006).

Contrary to the desert locust, which mainly inhabits desert areas during recession periods, the Senegalese grasshopper inhabits Sahelian cropping areas and rangelands. In these areas, biotopes on

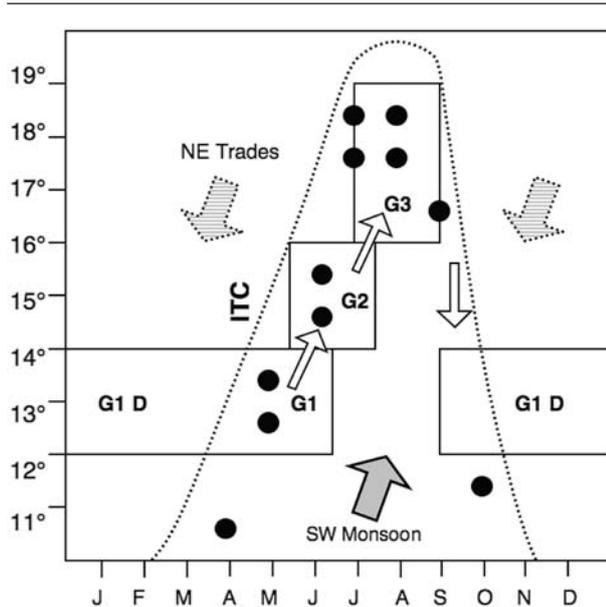


Figure 5 Conceptual diagram of the Senegalese grasshopper lifecycle and migrations in West Africa (modified from Lecoq 1995). **G1, G2, G3:** successive generations; **G1D:** diapaused G1 eggs; **ITC:** latitudinal position of the intertropical convergence zone; white arrows: adult migration direction; grey arrows: wind direction; black dots: conditions suitable for Senegalese grasshoppers for a given month and latitude.

sandy soils are utilized or not according to rainfall conditions, which are responsible for making them more or less suitable (optimal, too humid or too dry). The use of remote sensing to locate these areas has already generated encouraging results. In Senegal, by comparing normalized difference vegetation index (NDVI) map data with field data collected from May to August, positive correlations between the emergence of herbaceous vegetation, the presence of different acridian species and NDVI values ranging from 0.08 to 0.13 were noted (Cavin & Philips 1987 in Tappan *et al.*, 1991). Tappan & Moore (1989), Tappan *et al.* (1990, 1991) and Bergès *et al.* (1992) demonstrated that grasshopper outbreaks could be surveyed and forecasted on the basis of NOAA (NDVI) data. Bergès *et al.* (l.c.) established NDVI thresholds under which grasshopper populations are low. For the periods considered, Senegalese grasshopper outbreaks were found to overlap areas identified as being suitable on NDVI maps. More recently, Burt *et al.* (1995, 1997) suggested that METEOSAT IR channel data (to estimate rainfall) could be used to predict grasshopper outbreaks that could occur in the Sahel 2–3 weeks later, so it is a useful grasshopper treatment decision support tool. These tools are currently being used by the AGRHYMET centre in Niamey to monitor ecological conditions suitable for pest locust development (including Senegalese grasshoppers) so as to be able to issue alert bulletins if necessary (Traore *et al.* 2004). The data obtained can be used to monitor ecological conditions, but the link with the acridian risk is still estimated in a relatively empirical way, and further research is required to overcome this constraint.

The mathematical models

As early as 1990, Cheke reviewed knowledge on the lifecycle of *O. senegalensis* in West Africa, with an analysis of a model of migration phenomena. However, according to the author, quantitative grasshopper biology data were lacking at that time for the model.

Coop *et al.* (1991) constructed a decision support system for the economic analysis of Senegalese grasshopper control treatments in the Sahel which consisted of a grasshopper population dynamics simulation model. This model (GHLSIM) is based on the ecological model of Launois (1978b, 1979) and can be used to simulate population densities. This model was combined with a harvest loss module and a control campaign economic analysis module. However, this model did not account for one essential factor, i.e. north-south migrations of grasshopper populations.

In 1996, whereas the Launois model (1978b) was based on the hypothesis that rainfall and associated

migrations were key factors to explain outbreaks, Holt & Colvin mainly focused on predation. They presented data on the high level of egg predation and proposed a model of interactions between Senegalese grasshopper populations and predators using Lotka-Volterra equations, modified to integrate seasonal habitat variations. This model only distinguishes between two areas, i.e. northern and southern Sahel, which are linked by migrations. Population dynamics were studied relative to migrations, seasonal habitat changes and predation levels. Migration between areas and a high egg abundance in the dry season led to greater predator population stability and decreased grasshopper populations during the rainy season. The authors concluded that it is possible that mechanisms (migration and embryonic diapause) that are often considered as being an adaptation to seasonal habitat changes, could actually reduce outbreak risks rather than increase them. When these mechanisms are stalled, e.g. after an exceptional drought leading to high mortality in the grasshopper population, but also in the predator population, there is a higher outbreak risk (Colvin & Holt 1996; Holt & Colvin 1997).

Another model that simulates the dynamics of Senegalese grasshopper ecosystems was recently developed (Axelsen, *pers. com.*; Fisker *et al.* 2007). It simulates grasshopper population dynamics in five areas located along a south-north gradient and migrations between these areas. For each area, the model simulates the growth of millet, Senegalese grasshoppers, another secondary acridian (*Acrotylus blondeli*), two acridian egg predator species (bombylid, tenebrionid) and 24 birds that prey on acridians. This model is based mainly on rainfall levels, using data from meteorological stations as input. It can integrate the impact of grasshopper control measures. This model – which is calibrated on the basis of field data from Niger and Senegal – was used to simulate and study the respective roles of natural egg predators and bird predators. The simulations showed that the acridian population was reduced by 20–25% due to bird predation and by 15–20% as a result of egg predators during the rainy season. Long-term simulations (5 years) revealed that birds and egg predators caused an acridian population reduction of 80–97% (30–75% and 70–95%, respectively), thus highlighting that natural enemies have a major role in controlling this insect (Axelsen, *pers. com.*).

2. Economic impact and control strategies

Crop damage

Despite the fact that Popov, in Nigeria in 1970,

estimated that *O. senegalensis* was a species of very little economic importance, it is now considered to be the main chronic pest acridian in the Sahel. The serious outbreaks of this species (and of a few other often associated acridians) which occurred in 1974 and 1975 heightened awareness on the economic importance of this species. At that time, outbreaks were widespread in the West African Sahel region, affecting around 3 500 000 ha of cropland. Crop losses were estimated at around 368 000 t of cereals (Lecoq 1978b; Bernardi 1986). Since then, *O. senegalensis* has maintained its status as the main Sahelian pest (Cheke 1990). Major damage was recorded in 1974, 1975, 1977, 1978 and 1980, and then again in 1985, 1986, 1988 and 1989.

The extent of the problem varies between countries and years. For instance, control operations (aerial and terrestrial) against grasshoppers (mainly Senegalese grasshoppers) were conducted over an area of 3 385 000 ha in 1986 throughout the Sahel (FAO 1986 in Popov, 1996; Cheke 1990), 3 500 000 ha in 1989 and 1 000 600 ha in 1991, over a 4–6 month cropping season. In 1986–87, around 5 million ha were treated against *O. senegalensis*, for an overall cost of US\$60 million (Brader 1988). In 7 years, from 1986 to 1992, grasshopper control in the Sahel cost US\$177 million. Overall, in the last 20 years, grasshopper control was the main activity of crop protection services in Sahelian countries and the Senegalese grasshopper has become a chronic pest. Moreover, according to Singh & Bhatia (1965), Senegalese grasshoppers are sometimes associated with desert locust (*Schistocerca gregaria* Forskål) hoppers, thus facilitating the gregarization process in these locusts.

Senegalese grasshopper nymphs and adults mainly feed on wild and cultivated grasses (Boys 1978; Launois-Luong 1980). In the Sahel, graminaceous food crops (millet and sorghum) are mostly damaged (seeds and heads). They readily feed on the leaves but prefer seeds in the milky stage (Boys 1978).

At the onset of the rainy season, *O. senegalensis* destroys millet seeds, which may force farmers to resow their crops several times (Risbec & Mallamaire 1949; Bhatia & Ahluwalia 1967; OCLALAV 1973–1983; Popov 1976, 1988; McAleer 1977; Lecoq 1978b; Jago *et al.* 1993). At the end of the rainy season, major damage is noted on seeds in the milky stage (especially millet), which seem to attract sexually maturing females (Bhatia & Ahluwalia 1967; Boys 1978). Crop losses can thus be very high (Coop & Croft 1992, 1993). This is the period when these grasshoppers migrate southwards. In case of high outbreaks, massive concentrations of Senegalese grasshoppers, which are just as spectacular as gregarious locust swarms, can settle at night in ripening cereal crop fields and completely decimate them in a spectacular way within a few hours (Lecoq 1978b).

Several authors have reported crop loss estimates: 10–75% (mean 30%) in immature crops in India (Bhatia & Ahluwalia 1967); 20–40% millet, sorghum and rice yield losses in the Watagouna-Ansongo region of Niger (Cheke *et al.* 1980a); 70–90% losses at least once every 5 years in Mali (grasshoppers generally, including *O. senegalensis*) (Jago *et al.* 1993). Popov (1988) reported serious damage to millet crops in Senegal and Mali in 1974, in Nigeria and Niger in 1977, and in Mauritania in 1982. Other cereals such as maize, sorghum and wheat can also undergo major damage. In Nigeria, Hergert (1975) reported damage to sorghum and sugarcane crops. Some years even rangelands are attacked (COPR 1982).

Monitoring and control strategies

Lecoq & Mestre (1988), along with Diallo (1995), outlined the main steps for Senegalese grasshopper monitoring and control in Sahelian regions of West Africa: monitoring egg hatching at the onset of the rainy season, crop protection and surveys during the rainy season in northern Sahelian rangelands, and crop risk assessments during the period when grasshoppers migrate southwards, surveys and protection of ripening crops at the end of the rainy season, dry season surveys to assess diapaused egg densities and the potential risk for the following rainy season.

Many authors agree that Senegalese grasshopper control strategies should mainly be focused on managing juvenile populations, i.e. first instars hatched at the onset of the rainy season (which cause major damage to plantlets). This strategy, when carefully implemented – which is not always the case in most concerned countries – is generally known to be effective for considerably reducing primary populations, thus limiting the extent of movements and outbreaks for the rest of the rainy season, consequently reducing millet head damage induced by G3 adults at the end of the season (Saraiva 1962; Fishpool 1982; Popov 1988; Cheke 1990).

To implement this strategy, sites where there are high early instar concentrations must be quickly pinpointed and be the main treatment target. Diapaused egg fields thus have to be accurately detected. Dry season surveys carried out by crop protection services can detect areas where there are high egg-pod concentrations. Shah *et al.* (2000) proposed a sampling method to assess egg-pod densities with a relatively high degree of accuracy. Monitoring between March and June would be difficult since this is the period when farmers are involved in preparing their fields for the next cropping season. The only period possible for such assessments would be from December to February. Modder (1986) and

Shah *et al.* (2000) suggested financially compensating farmers in order to get enough people involved in these survey operations. Rapidly locating areas with suitable rainfall conditions at the onset of the monsoon season on the basis of field and remote-sensing data could enhance control of just-hatched nymphs (Burt *et al.* 1995, 1997).

However, considering the vast areas concerned, the material and human resources mobilized would need to be boosted substantially. Due to current difficulties in implementing this preventive strategy, crop protection services often have to deal with outbreaks at the end of the cropping season. Infestations at this time can be very serious and rapid, so treatments have to be much heavier to be able to protect the ripening crops.

Non-chemical control methods

Non-chemical control methods have been regularly proposed by Saraiva (1962) and Amatobi *et al.* (1986, 1988, 1991). These authors recommended, amongst other methods, weeding, intensive tillage, flooding egg fields, reforestation and field consolidation. Saraiva (1962), in Cape Verde, recommended trapping grasshoppers using fresh maize stems, and then burning them or destroying them with pesticides. Fishpool (1982) recommended temporarily stopping weeding for the period when plantlets are seriously attacked by hoppers, which could help to reduce damage. Another approach involves using resistant varieties. It was pointed out that in India there is a variety of millet (*P. glaucum*) with heads covered with long bristles that protect them from Senegalese grasshopper attacks (Bhatia & Ahluwalia 1967). Tilling the soil to destroy egg pods does not seem to be an effective control method (Popov 1980; Cheke 1990), except perhaps locally (Shah *et al.* 2000).

These various control measures proposed are often contradictory, difficult to implement and hard to reconcile with other production imperatives. A critical study to assess their efficacy, economic impact and compatibility with other common agricultural practices should be conducted before implementing them in farmers' fields. Stonehouse *et al.* (1997) also showed that very few grasshopper control operations in the Sahel were carried out by farmers because of the time and money costs – these mainly involved chemical treatments conducted by crop protection services or village teams.

Chemical control methods

Chemical pesticide treatment is currently the main technique used to control acridians, especially Senegalese grasshoppers.

Simple cost-effective techniques have been recommended to enable farmers to control hoppers themselves. This includes dusting of powdered pesticides (Popov 1980), the use of poisoned bran-based bait, and ultra low volume (ULV) pesticide spraying (Cheke 1990). However, on the basis of test results, Jago *et al.* (1993) does not recommend promoting or subsidising ULV pesticide treatments to control millet pests (including Senegalese grasshoppers) in farmers' fields in Mali. According to these authors, this technique does not warrant widespread use because of the low economic return.

Adult concentrations can also be controlled on a small scale by farmers at the end of the rainy season. However, in cases of serious outbreaks, more large-scale terrestrial and aerial operations are generally required, with hundreds of thousands of hectares sometimes treated. Such large-scale treatments are often beyond the capacity of the affected countries and are partially subsidized by the international community.

Joyce (1983) suggested that the best period for treating these pests was to take advantage of their high flight concentrations during nocturnal migrations following the seasonal movement of the ITCZ. Riley & Reynolds (1990), along with Drake & Farrow (1988), noted that flying insect densities are often 100-fold greater in convergence zones. However, they showed that targeting such flying insects (especially at night) with pesticide sprays would be very hard to manage: less than 30% of flying grasshoppers seem to be concentrated in convergence zones and air surveys to pinpoint sites where there are such concentrations would necessitate the simultaneous use of at least two aircraft per 500 km².

Negative impacts of pesticide treatments

Chemical control is the only strategy currently used, but there are various associated problems involved, especially financial. Every year, substantial efforts are mobilized, often through support from donor countries, to spray high quantities of chemical pesticides to protect Sahelian farmers' meager crops. But there is a question as to how long the development partners will be ready to support such very expensive operations (Sidibe 1998), especially that no real cost-effectiveness analyses are generally carried out. In addition, this practice increases the dependency of farmers' and crop protection services on using free pesticides (Kremer & Lock 1992). Finally, these chemical products have a clear environmental impact, and this aspect is being highlighted to an increasing extent. This especially involves negative impacts on nontarget fauna and natural enemies of grasshoppers, which are required

for long-term regulation of grasshopper populations and to hamper outbreaks (Greathead 1992). The extent to which predators and parasitoids are able to regulate grasshopper population dynamics has yet to be clearly determined. It is generally thought that meteorological factors and migrations have a key role (Greathead 1992), especially with respect to species like desert locusts. However, the impact could be greater in more sedentary species, i.e. that generally do not migrate long distances (cf. Belovski & Joern 1995), and pesticides could turn out to be detrimental in the long term. But the development of pesticide resistance in African grasshoppers has never been documented.

Niassy *et al.* (1993), in pesticide treated areas, still found that acridian egg parasitism rates were significantly higher in comparison to rates in untreated areas. According to these authors, pesticide treatments likely kill off the primary natural enemies of egg predators and parasites.

However, it is generally suspected that the overfrequency of treatments could seriously limit the impact of natural enemies, reduce the natural control of grasshopper populations and promote an increase in the outbreak frequency and size. The first personal observations in Niger (Maiga, in preparation) clearly revealed that regularly treated areas had significantly lower natural enemy populations. Van der Valk *et al.* (1999) studied the impact of pesticide treatments on populations of Senegalese grasshoppers and *Kraussaria angulifera* (Krauss) grasshoppers and showed that the use of broad spectrum pesticides for controlling grasshoppers detected at the onset of the rainy season could increase populations of grasshoppers detected late the following year.

Alternative control methods

These problems have prompted spectacular development of alternative methods in the last two decades that involve the use of entomopathogenic protozoans and fungi.

Trials were conducted with the protozoan *Nosema locustae* Canning on *O. senegalensis* as early as 1982 in northern Senegal, but the results were not conclusive (Fishpool, *in* Diop 1997). Tests carried out in Cape Verde and Mauritania with *N. locustae* spore-based bait revealed that most acridian species, including *O. senegalensis*, were infected (Henry *et al.*, 1985). Significant mortality was obtained in a test with the fungus *Beauveria bassiana* (Balsamo) Vuillemin (Lima *et al.* 1992). *B. bassiana* strains BF 49 and BF 129, respectively isolated from soil and grasshopper samples, were found to be effective against *O. senegalensis* in the laboratory and the field in the Sahel (Ouedraogo 1993).

The fungus *Metarhizium anisopliae* var. *acridum* has been the focus of many investigations in the last 15 years or so, and it currently seems to be the most promising alternative to chemical control. This fungus was noted for the first time at Sadoré, Niger, in 1988 on *Ornithacris cauroisi* (Finot 1907) fledgelings, and the population of this grasshopper had been almost completely decimated. Very encouraging results have been obtained since then in both the laboratory and field, showing high efficacy in controlling acridians and the Senegalese grasshopper (Langewald *et al.* 1999; Maiga *et al.* 1998). A formulation has already been produced in South Africa with this entomopathogenic fungus, and it is marketed under the name Green Muscle®. Commercial production is being planned in the Sahel. Grasshoppers infected with this pathogen can, however, modify their thermoregulatory behaviour, which could be a constraint to its use and limit its impact under certain environmental conditions (Blanford *et al.* 1998). In addition, a strategy to use such pathogen products has yet to be developed, but it has to be kept in mind that they are slow to act and thus cannot be used in emergency situations on immediately threatened crops.

A model was recently used to simulate the impact of various grasshopper control strategies, using chemical pesticides or a mycopesticide, on crop yields and the environment (Axelsen, *pers. com.*; Fisker *et al.* 2007). A cost-effectiveness analysis showed that the most efficient strategy involved a combination of treatments using a mycopesticide in the southern part of the distribution range at the onset of the rainy season, along with chemical pesticide treatments in all areas where there was a density of over 40 grasshoppers per square metre. This strategy – which should be applied yearly in order to be cost-effective – minimizes crop losses and safeguards millet production locally and throughout the area. The initial results also suggest that these mycopesticide-based preventive treatments, in grassy savanna areas and in millet crop fields in the southern part of the distribution range, is more environment-friendly than chemical treatments conducted only in millet fields throughout the area. However, other factors such as bombilid fly densities and the presence of alternative prey for bird predators of grasshoppers also have to be taken into consideration when comparing mycopesticide and chemical pesticide treatments (Axelsen, *pers. com.*). Further studies are now required to determine whether such a preventive strategy involving large-scale treatments outside of crop fields would be operationally feasible.

Finally, a recent study try to evaluate the importance of residual effects from previous years' treatment on

the efficiency of different strategies for control of *O. senegalensis* with *M. anisopliae* var. *acidum*. Data from two field studies indicate that second year effects on grasshopper control with *M. anisopliae* can occur at levels that are important for overall efficiency of the control operations. Simulations made with the model system of Fisker *et al.* (2007), which can calculate the efficiency of different grasshopper control strategies, indicate that the second year effect of *M. anisopliae* is most important in a repetitive treatment strategy, where control operations are concentrated in the main millet production area (Bak *et al.*, 2007). However, the importance of second year effects should be included in risk assessment of *M. anisopliae*, since the effect was also found in non-target species.

Conclusions

Substantial progress has been made over the last 30 years on gaining insight into the ecology of Senegalese grasshoppers, monitoring grasshopper situations and forecasting outbreak risks. However, the impact of natural enemies seems to have been overlooked or is not yet understood. It is now essential to clarify their role, especially that the only present response to outbreaks, which are now chronic, is massive chemical pesticide treatments, but the potential detrimental long-term impacts of such treatments have yet to be thoroughly assessed.

In the short term, control measures should be enhanced, particularly by improving monitoring and increasing the quality and number of surveys to locate outbreak hotspots and diapaused egg fields during the dry season. In the medium term, biological grasshopper control products that have been tested in recent years should now be used (at least partially) as an alternative to chemical pesticides – but a clear realistic strategy first has to be developed.

References

- Ahluwalia P.J.S., Sikka H.L., Venkatesh M.V. 1976. Behaviour of swarms of *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae: subfamily Oedipodinae). *Indian Journal of Entomology* **38**: 114-117.
- Amatobi C.I. 1985. Oviposition preference and the influence of cultivation on egg hatching in *Oedaleus senegalensis* K. *Samaru Journal of Agricultural Research* **3**: 81-85.
- Amatobi C.I., Apeji S.A., Oyidi O. 1986. Weeding as a means of reducing the population of grasshopper pests and damage on pearl millet (*Pennisetum americanum* (L.) K. Schaum) in Northern Nigeria. *Insect Science and its Application* **7**: 99-102.
- 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. *Tropical Pest Management* **34**: 173-179.
- Amatobi C.I., Apeji S.A., Oyidi O. 1991. Field observation on the diurnal activities of the sahelian plague grasshopper *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae) in Northern Nigeria. *Nigerian Journal of Entomology* **7**: 1-19.
- Amene C., Vajime C.G. 1990. Parasites, parasitoids and predators of *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae) in Nigeria. *Insect Science and its Application* **11**: 27-34.
- Arnaud M., Forest F., Launois M. 1982. Automatisation d'un modèle écologique original propre à *Oedaleus senegalensis* (Krauss, 1877) (Orthoptera: Acrididae). *Agronomie Tropicale* **37**: 159-171.
- Bak J., Fisker E.N., Kooyman C. 2007. Evaluating the importance of residual effects from previous years' treatment on the efficiency of different strategies for control of Sahelian grasshoppers with *Metarhizium anisopliae* var. *acidum*. *Biocontrol Science and Technology* **17**: 413-422.
- Batten A. 1969. The senegalese grasshopper *Oedaleus senegalensis* Krauss. *Journal of Applied Ecology* **6**: 27-45.
- Bhatia D.R., Ahluwalia P.J.S. 1962. Swarming of *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae) in Rajasthan-India. *Indian Journal of Entomology* **24**: 22.
- Belovsky G.E., Joern A. 1995. The dominance of different regulating factors for rangeland grasshoppers, p. 359-386 in: Cappuchino N., Price P.W. (eds). *Population Dynamics. New Approaches and Synthesis*. Academic Press, San Diégo, USA.
- Bhatia D.R., Ahluwalia P.J.S. 1967. *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae Subfamily Oedipodinae) plague in Rajasthan. *Plant Protection Bulletin* (New Delhi) **18**: 8-12.
- Berges J.C., Chiffaud J., Mestre J. 1992. Apport de la télédétection spatiale à l'identification des zones favorables pour le Criquet sénégalais au Sahel. *Veille climatique satellitaire* **40**: 25-33.
- Bernardi M. 1986. Le problème des sauteriaux, p. 43-57 in: *Compte rendu du séminaire international du projet CILSS de lutte intégrée, Niamey, Niger. 6-13 décembre 1984*. CILSS, Niamey.
- Blanford S., Thomas M.B., Langewald J. 1998. Behavioural fever in the Senegalese grasshopper, *Oedaleus senegalensis*, and its implications for biological control using pathogens. *Ecological Entomology* **23**: 9-14.
- Bolivar I. 1889. Orthopteros de Africa del Museo de Lisboa. Part I. *Jornal de Sciencias Mathematicas, Physicas e Naturaes, Academia Real das Sciencias de Lisboa, Segunda Série, 1*: 73-112.
- Boys H.A. 1978. Food selection by *Oedaleus senegalensis* (Acrididae: Orthoptera) in grassland and millet fields. *Entomologia Experimentalis et Applicata* **24**: 78-86.
- Brader L. 1988. Control of grasshoppers and migratory locusts. *British Crops Protection Council* **1**: 283-288.
- Burt P.J.A., Colvin J., Smith S.M. 1995. Remote sensing of rainfall by satellite as an aid to *Oedaleus senegalensis* (Orthoptera: Acrididae) control in the Sahel. *Bulletin of Entomological Research* **85**: 455-462.
- Burt P.J.A., Colvin J., Smith S.M. 1997. Forecasting the early-season eclosion of *Oedaleus senegalensis* in the Sahel: the role of remotely sensed rainfall data, p. 55-61 in: Krall S., Peveling R., Diallo D. Ba (eds), *New Strategies in Locust Control*. Birkhäuser Verlag, Basel, Switzerland.
- Chandra S. 1982. Screening of some desert plants feeding preference in *Oedaleus senegalensis* (Orthoptera: Acrididae, subfamily Oedipodinae). *Plant Protection Bulletin* (New Delhi) **34**: 15-17.
- Chandra S. 1983. Some field observations on a small concentration of *Oedaleus senegalensis* (Orthoptera: Acrididae) in the Indian desert. *Plant Protection Bulletin* (New Delhi) **35**: 9-13.
- Cheke R.A. 1990. A migrant pest in the Sahel: the senegalese grasshopper *Oedaleus senegalensis* K. *Philosophical Transactions of the Royal Society of London* **328**: 539-553.

- Cheke R.A., Fishpool L.D., Forrest G.A. 1980a.** *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. 1980b.** An ecological study of the egg-pods of *Oedaleus senegalensis* (Krauss) (Orthoptera: Acrididae). *Journal of Natural History* **14**: 363-371.
- Chiffaud J., Mestre J. 1991.** Reconnaissance des oothèques d'acridiens. Apport des données anatomiques de l'appareil reproducteur. *Sabel PV Info* **31**: 2-3.
- Chopard L. 1950.** Contribution à l'étude de l'Air. Orthopteroïdes. *Mémoires de l'Institut Français d'Afrique Noire* **10**: 127-145.
- Colvin J. 1996.** Diapause duration, survival in relation to desiccation and egg-pod morphology of the Senegalese grasshopper, *Oedaleus senegalensis*. *Physiological Entomology* **21**: 173-178.
- Colvin J. 1997.** Biotic and abiotic factors affecting the population dynamics of the Senegalese grasshopper, *Oedaleus senegalensis*, p. 63-67 in: **Krall S., Peveling R., Diallo D. Ba (eds)**, *New Strategies in Locust Control*. Birkhäuser Verlag, Basel, Switzerland.
- Colvin J., Cooter R.J. 1995.** Diapause induction in the Senegalese grasshopper, *Oedaleus senegalensis*. *Physiological Entomology* **20**: 13-17.
- Colvin J., Holt J. 1996.** Modèle d'étude des effets de la pluviométrie, de la prédation et de la quiescence des oeufs sur la dynamique des populations du criquet sénégalais, *Oedaleus senegalensis*. *Science et changements planétaires/ Sécheresse* **7**: 145-150.
- Coop L.B., Croft B.A. 1992.** Damage rates to pearl millet by adults of grasshopper species and *Psalydolytta* blister beetles in Mali. *Tropical Pest Management* **38**: 201-205.
- Coop L.B., Croft B.A. 1993.** Pearl millet injury by five grasshopper species (Orthoptera: Acrididae) in Mali. *Journal of economic entomology* **86**: 891-898.
- Coop L.B., Croft B.A., Murphy C.E., Miller S.F. 1991.** Decision support system for economic analysis of grasshopper treatment operations in the African Sahel. *Crop protection* **10**: 485 - 495.
- COPR 1982.** *The locust and grasshopper agricultural manual*. Centre for Overseas Pest research, London, 690 p.
- Dahdouh B., Duranton J.F., Lecoq M. 1978.** Analyse des données sur l'écologie des acridiens d'Afrique de l'Ouest. *Les cahiers de l'analyse des données* **3**: 459-482.
- Davey J.T., Descamps M., Demange R. 1959.** Notes on the Acrididae of french Sudan with special reference to Central Niger Delta. Part II. *Bulletin de l'Institut Français d'Afrique Noire* **21**: 565-600.
- Descamps M. 1953.** Observations relatives au criquet migrateur africain et à quelques autres espèces d'Acrididae du Nord Cameroun. *Agronomie Tropicale* **8**: 567-613.
- Descamps M. 1975.** *Visite d'expert-conseil dans le bassin Tchadien. Etudes biologiques. Recherches sur le criquet migrateur africain*. PNUD/FAO RAF 69/146. FAO, Rome, 14 p.
- Diallo B.D. 1995.** Protection des végétaux dans le Sahel: surveillance et prospection, p. 15-25 in: *International symposium on agricultural pest forecasting and monitoring. Proceedings*. Québec, 10-13 October 1995.
- Dingle H. 1980.** *Ecology and evolution of migration*, p. 1-101 in: **Gauthreaux S.A. (ed.)**, *Animal migration, orientation, and navigation*. Academic Press, New York.
- Dingle H. 1986.** Evolution and genetics of insect migration, p. 11-26 in: **Danthanarayana W. (ed.)**, *Insect flight: dispersal and migration*. Springer-Verlag, Berlin.
- Diop T. 1987.** *Contribution à l'étude de la dynamique des populations d'acridiens dans la vallée du Sénégal*. Thèse de Doctorat, Université de Paris VI, Paris, 154 p.
- Diop T. 1993.** Observations préliminaires sur le rôle de la photopériode sur la diapause embryonnaire du criquet sénégalais, *Oedaleus senegalensis* (Krauss, 1877). *Insect Science and its Application* **14**: 471-475.
- Diop T. 1995.** Effet de la photopériode sur l'induction de la diapause embryonnaire du criquet sénégalais *Oedaleus senegalensis* K. *Journal of African Zoology* **109**: 161-172.
- Diop T. 1997.** Inventaire commenté de la bibliographie sur le criquet sénégalais *Oedaleus senegalensis* K. *Insect Science and its Application* **17**: 227-291.
- Drake V.A., Farrow R.A. 1988.** The influence of atmospheric structure and motions on insect migration. *Annual Review of Entomology* **33**:183-210.
- Duranton J.F., Launois M., Launois-Luong M.H., Lecoq M. 1979.** Biologie et écologie de *Catantops haemorrhoidalis* Krauss en Afrique de l'Ouest. *Annales de la Société entomologique de France* (n.s.) **15**: 319-343.
- Duranton J.F., Launois M., Launois-Luong M.H., Lecoq M. 1983.** Contribution à l'inventaire faunistique des Acridiens de l'archipel du Cap Vert. *Bulletin de la Société entomologique de France* **88**: 197-224.
- Duranton J.F., Launois M., Launois-Luong M.H., Lecoq M. 1984.** Nouvelle contribution à l'inventaire faunistique des Acridiens de l'Archipel du Cap Vert. Signalisation du genre *Wernerella* Karny 1907 et description de *Wernerella atlantica* POPOV n. sp. (Orth. Acrididae). *CFS-Courier ForschungsInstitut Senckenberg* (Frankfurt am Main) **68**: 39-47.
- Duranton J.F., Lecoq M. 1980.** Ecology of locusts and grasshoppers (Orthoptera, Acrididae) in Sudanese West Africa. 1. Discriminant factors and ecological requirements of acridian species. *Acta Oecologica* **1**: 151-164.
- Duviard D. 1973.** Les vols migratoires de *Dysdercus völkeri* Schmidt (Hemiptera: Pyrrhocoridae) en Côte d'Ivoire. *Coton et Fibres Tropicales* **28**: 239-252.
- FAO 2006.** *L'observatoire acridien. Groupe acridien et autres migrants nuisibles*. FAO, Roma. <http://www.fao.org/ag/locusts/fr/activ/DLIS/satel/index.html> (on line) (access January 2007)
- Farrow R. 1977.** Origin and Decline of the 1973 Plague Locust Outbreak in Central Western New South Wales. *Australian Journal of Zoology* **25**: 455-489.
- Farrow R. 1979.** Population dynamics of the Australian plague locust, *Chortoicetes terminifera* (Walker), in central western New South Wales. I. Reproduction and migration in relation to weather. *Australian Journal of Zoology* **27**: 717-745.
- Fishpool L.D. 1982.** The ecology of the west african grasshopper fauna of the sahel and sudan savanna with special reference to *Oedaleus senegalensis*. Ph. D. Dissertation, University of London, 442 p.
- Fishpool L.D.C., Cheke R.A. 1983.** Protracted eclosion and viability of *Oedaleus senegalensis* (Krauss) eggs (Orthoptera, Acrididae). *Entomologist's monthly magazine* **119**: 215-219.
- Fisker E.N., Bak J., Niassy A. 2007.** A simulation model to evaluate control strategies for the grasshopper *Oedaleus senegalensis* in West Africa. *Crop Protection* **26**: 592-601.
- Garba Y. 1998.** *Rôle de l'occupation des sols sur le peuplement acridien de la région de Banizoumbou (Niamey, Niger)*. Thèse de doctorat, Université de Paris XI, Paris, 219 p.
- Gehrken U., Doumbia Y.O. 1996.** Diapause and quiescence in eggs of a tropical grasshopper *Oedaleus senegalensis* (Krauss). *Journal of Insect Physiology* **42**: 483-491.
- Golding F.D. 1934.** On the ecology of Acrididae near Lake Chad. *Bulletin of Entomological Research* **25**: 263-303.
- Golding F.D. 1948.** The Acridinae (Orthoptera) of Nigeria. *Transactions of the Royal entomological Society of London* **99**: 517-587.
- Greathead D.J. 1963.** A review of the insect enemies of Acridoidea (Orthoptera). *Transactions of the Royal entomological Society of London* **114**: 114-437.
- Greathead D.J. 1992.** Natural enemies of tropical locusts and grasshoppers: their impact and potential as biological agents, p. 105-112 in: **Lomer C.J., Prior C. (eds)**, *Biological control of locusts and grasshoppers*. CAB International, Oxon, UK.

- Henry J.E., Wilson M.C., Oma E. A., Fowler J. L. 1985. Pathogenic micro-organisms isolated from west African grasshoppers (Orthoptera: Acrididae). *Tropical Pest Management* **31**: 192-195.
- Hergert C.R. 1975. An analysis of grasshoppers problems in Kano State. *Samaru. Agricultural Newsletter* **17**: 91-94.
- Hielkema J.U. 1991. Desert locust monitoring with satellite remote sensing. *ITC Journal* 1981-4: 387-417.
- Hielkema J. U., Ayyangar R. S., Sinha P.P. 1981. Satellite remote sensing, a new dimension in international Desert locust survey and control. *FAO Plant Protection Bulletin (English Ed.)* **33**: 165-173.
- Hielkema J. U., Roffey J., Tucker C.J. 1986. Assessment of ecological conditions associated with the 1980/81 desert locust plague upsurge in West Africa using environmental satellite data. *International Journal of Remote Sensing* **7**: 1609-1622.
- Holt J., Colvin J. 1997. A differential equation model of the interaction between the migration of the Senegalese grasshopper, *Oedaleus senegalensis*, its predators, and a seasonal habitat. *Ecological Modelling* **101**: 185-193.
- Hughes R.D. 1979. Movement in population dynamics, p. 14-34 in: Rabb R.L., Kennedy G.G. (eds), *Movement of highly mobile insects: concepts and methodology in research*. N. Carolina St. Univ. Raleigh, North Carolina, USA.
- Jago N.D. 1968. A Checklist of grasshoppers (orthoptera, Acrididae) recorded from Ghana, with biological notes and extracts from the recent literature. *Transactions of the American Entomological Society* **94**: 209-353.
- Jago N.D. 1983. Light trap sampling of the grasshopper *Oedaleus senegalensis* (Krauss, 1877) (Acrididae: Oedipodinae) and other species in West Africa. A critique, p. 165-198 in: Tyrkus M., Cantrall I.J., Carbonell C.S. (eds), *Proceedings of the 2nd Triennial Meeting*, 21-25 July 1979. Pan American Acridological Society, Bozeman, USA.
- Jago N.D., Kremer A.R., West C. 1993. *Pesticides on Millet in Mali*. *NRI Bulletin*, **50**, Natural Resources Institute, Chatham, UK, 46 p.
- Joyce R.J.V. 1952. The ecology of grasshoppers in East Central Sudan. *Anti Locust Bulletin* **11**: 1-103.
- Joyce R.J.V. 1983. Aerial transport of pests and pest outbreaks. *EPPO Bulletin* **13**: 111-119.
- Kremer A.R., Lock C. 1992. A decision model for sponsors of crop protection in the western Sahel. *Tropical Science* **32**: 397-419.
- Langewald J., Ouambama Z., Mamadou A., Peveling R., Stolz I., Bateman R., Blanford S., Arthurs S., Attignon S., Lomer C. 1999. Comparison of an organophosphate insecticide with a mycoinsecticide for the control of *Oedaleus senegalensis* (Orthoptera: Acrididae) and other Sahelian grasshoppers at an operational scale. *Biocontrol Science and Technology* **9**: 199-214.
- Launois M. 1978a. *Manuel pratique d'identification des principaux acridiens du Sahel*. Ministère de la coopération, Paris, 256 p.
- Launois M. 1978b. *Modélisation écologique et simulation opérationnelle en acridologie. Application à Oedaleus senegalensis K.* Ministère de la coopération, Paris et GERDAT, Montpellier, France, 212 p.
- Launois M. 1979. An ecological model for the study of the grasshopper *Oedaleus senegalensis* in West Africa. *Philosophical Transactions of the Royal Society of London* **287**: 345-355.
- Launois M. 1984. *Une approche pragmatique de la modélisation écologique: les biomodèles à géométrie variable*. Centre de coopération internationale en recherche agronomique pour le développement, Montpellier, France, 58 p.
- Launois M., Launois-Luong M.H. 1989. *Oedaleus senegalensis (Krauss, 1877), sauteriaux ravageur du Sahel. Collection Acridologie Opérationnelle*, **4**, CILSS-DFPV, Niamey, Ministère des Affaires étrangères des Pays-Bas, La Haye, CIRAD, Montpellier, 72 p.
- Launois M., Lecoq M. 1990. Biomodélisation et stratégies de lutte antiacridienne en Afrique et à Madagascar. *Mededelingen van de Faculteit landbouwwetenschappen Rijksuniversiteit Gent* **55**: 225-234.
- Launois M., Launois-Luong M.H., Lecoq M. 1988. Fauna Cabo-Verdiana: Catalogue des Acridiens de l'Archipel du Cap-Vert (Insectes - Orthoptères - Caelifères). *Courier Forschungsinstitut Senckenberg (Frankfurt am Main)* **105**: 155-163.
- Launois M., Launois-Luong M.H., Lecoq M. 1996. Sécheresse et survie des sauteriaux du Sahel ouest africain. *Science et changements planétaires/ Sécheresse* **7**: 119-127.
- Launois-Luong M.H. 1979a. Etude de la production des œufs d'*Oedaleus senegalensis* (Krauss) au Niger (Région de Maradi). *Bulletin IFAN* **41**: 128-148.
- Launois-Luong M.H. 1979b. Etude comparée de l'activité génésique de sept acridiens du Sahel dans des conditions éco-météorologiques semblables. *Annales de Zoologie Ecologie Animale* **1**, 202-226.
- Launois-Luong M.H. 1980. Etude expérimentale des potentialités de dégâts des principaux acridiens du sahel. *Bulletin de l'Institut Fondamental d'Afrique Noire* **41**: 774-814.
- Launois-Luong M.H., Lecoq M. 1989. *Vade-mecum des Criquets du Sahel*. Collection Acridologie Opérationnelle **5**. CILSS-DFPV, Niamey, Ministère des Affaires étrangères des Pays-Bas, La Haye, CIRAD, Montpellier, 126 p.
- Lecoq M. 1978a. Biologie et dynamique d'un peuplement acridien de zone soudanienne en Afrique de l'Ouest. *Annales de la Société entomologique de France (n.s.)* **14**: 603-681.
- Lecoq M. 1978b. Le problème sauteriaux en Afrique soudano-sahélienne. *Agronomie Tropicale* **33**: 241-258.
- Lecoq M. 1978c. Les déplacements par vol à grande distance chez les acridiens des zones sahélienne et soudanienne en Afrique de l'Ouest. *Comptes rendus de l'Académie des Sciences* **284**: 419-22.
- Lecoq M. 1984. Ecology of locusts and grasshoppers (Orthoptera, Acrididae) in Sudanese West Africa. 2. Ecological niches. *Acta Oecologica* **5**: 229-242.
- Lecoq M. 1988. *Les Criquets du Sahel. Collection Acridologie opérationnelle*, **1**, CILSS-DFPV, Niamey, Ministère des Affaires étrangères des Pays-Bas, La Haye, CIRAD, Montpellier, 129 p.
- Lecoq M. 1995. Forecasting systems for migrant pests. III. Locusts and grasshoppers in West Africa and Madagascar, p. 377-395 in: Drake V.A., Gatehouse A.G. (eds), *Insect migration: physical factors and physiological mechanisms*. Cambridge University Press, Cambridge.
- Lecoq M., Mestre J. 1988. *La surveillance des sauteriaux du sahel. Collection Acridologie opérationnelle*, **2**, CILSS-DFPV, Niamey, Ministère des Affaires étrangères des Pays-Bas, La Haye, CIRAD, Montpellier, 62 p.
- Lima M.L.L., Brito J.M., Henry J.E. 1992. *Biological control of grasshoppers in the Cape Verde Islands*. CAB International. National Institute for Agricultural research, Praia, Cape Verde.
- Maiga I.H., Douro-Kpindou O.K., Lomer C.J., Langewald J. 1998. Utilisation de *Metarhizium flavoviride* Gams & Rozypal contre les sauteriaux dans des essais participatifs en milieu paysan au Niger. *Insect Science and its Application* **18**: 279-284.
- Mallamaire A. 1948. Acridiens migrateurs et acridiens sédentaires en Afrique occidentale. *Agronomie Tropicale* **3**: 630-634.
- McAleer I.P.B. 1977. *OSRO Plant Protection Project: Grasshopper Pests of the Sahel*. Centre for Overseas Pest research, London, 27 p.
- Mestre J. 1988. *Les acridiens des formations herbeuses d'Afrique de l'Ouest*. Ministère de la coopération, Paris et CIRAD, Montpellier, France, 331p.
- Modder W.W.D. 1986. An integrated pest management strategy for the African grasshopper *Zonocerus variegatus*. *The Nigerian Field* **51**: 41-52.
- Moizzuddin M. 1991. Studies of *Oedaleus senegalensis* (Krauss) (Orthoptera: Acrididae) with special reference to its habitat and genitalia. *Proceedings, Eleventh Pakistan Congress of Zoology* **1**: 107-117.
- Niassy A., Beye A., van der Valk H. 1993. *Impact des applications de fénitrothion sur la mortalité naturelle des oothèques de sauteriaux au Sénégal (traitements de 1991)*. FAO Projet ECO/SEN/003/LOCUSTOX. Direction de la protection des végétaux, Dakar, Sénégal.
- OCLALAV 1973-1983. *Rapports mensuels*. Organisation commune de lutte antiacridienne et de lutte antiaviaire, Dakar, Sénégal.

- Ouedraogo R. 1993.** *Investigations on the use of Beauveria bassiana against the senegalese grasshopper, Oedaleus senegalensis (Krauss 1877) (Orthoptera: Acrididae).* M.Sc. Dissertation, Simon Fraser University, Burnaby, British Columbia, Canada, 68 p.
- Pedgley D.E. 1980.** Weather and airborne organisms. World Meteorological Organisation *Technical. Notes World Meteorological Organization* 173.
- Popov G.B. 1976.** The 1974 outbreak of grasshoppers in western Africa, p. 35-43 in: *Report of the Sahel Crop Pest Management Conference.* USAID report. University of California, Berkeley.
- Popov G.B. 1980.** Studies of oviposition, egg development and mortality in *Oedaleus senegalensis* in the Sahel. *Centre for Overseas Pest Research Miscellaneous Report* 53: 1-48.
- Popov G.B. 1985.** *Résumé des travaux du projet de recherche et de vulgarisation COPR/OCALAV sur les sauteriaux du Sahel dans la moyenne vallée du Niger.* Stations de recherches acridiennes sur le terrain. Séries techniques. N° AGP/DL/T5/25. FAO, Rome, 123 p.
- Popov G.B. 1988.** Sahelian grasshoppers. *Overseas Development Natural Resources Institute Bulletin* 5: 1-87.
- Popov G.B. 1989.** *Nymphs of the Sahelian Grasshoppers.* Overseas Development Natural Resources Institute, Chatham, UK, 158 p.
- Popov G.B. 1996.** Quelques effets de la sécheresse sahélienne sur la dynamique des populations acridiennes. *Science et changements planétaires/ Sécheresse* 7: 91-98.
- Popov G.B., Launois-Luong M.H., Van Der Weel J.J. 1990.** *Les oothèques des criquets du Sahel. Collection Acridologie opérationnelle, 7,* CILSS-DFFV, Niamey, Ministère des Affaires étrangères des Pays-Bas, La Haye, CIRAD, Montpellier, 152 p.
- Rainey R.C. 1951.** Weather and the movements of locust swarms: a new hypothesis. *Nature, London* 168: 1057-1060.
- Rainey R.C. 1963.** Meteorology and the migration of Desert Locusts. Applications of synoptic meteorology in locust control. *Anti-Locust Memoirs* 7: 1-115 (also as Tech. Notes Wld met. Org. 54).
- Rainey R.C. 1976.** Flight behaviour and features of the atmospheric environment. *Symposia of the Royal entomological Society of London* 7: 75-112.
- Rainey R.C. 1979.** Dispersal and redistribution of some Orthoptera and Lepidoptera by flight. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 52: 125-132.
- Rankin M.A. 1985.** Introduction, p. 1-4 in: **Rankin M.A. (ed.).** *Migration: mechanisms and adaptive significance.* Marine Sci. Inst. (Contribution in marine Science, supplement vol. 7), Port Aransas, Texas, USA.
- Reynolds D.R., Riley J.R. 1988.** A migration of grasshoppers, particularly *Diablocatantops axillaris* (Thunberg) (Orthoptera: Acrididae), in the West African Sahel. *Bulletin of Entomological Research* 78: 252-271.
- Riley J.R., Reynolds D.R. 1979.** Radar-based studies of the migratory flight of grasshoppers in the middle Niger area of Mali. *Proceedings of the Royal Society of London Series B - Biological Sciences* 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. *Journal of Animal Ecology* 52: 167-183.
- Riley J.R., Reynolds D.R. 1986.** Orientation at night by high-flying insects, p. 71-87 in: **Danthanarayana W. (ed.),** *Insect flight: dispersal and migration.* Berlin, Springer-Verlag.
- Riley J.R., Reynolds D.R. 1990.** Nocturnal grasshopper migration in West Africa: transport and concentration by the wind, and the implications for air-to-air control. *Philosophical Transactions of the Royal Society of London Series B - Biological Sciences* 328: 655-672.
- Risbec J., Mallamaire A. 1949.** Les animaux prédateurs et les insectes parasites des riz cultivés en Afrique occidentale. *Agronomie Tropicale* 4: 70-76.
- Ritchie J.M. 1978.** Melanism in *Oedaleus senegalensis* and other oedipodines (Orthoptera, Acrididae). *Journal of Natural History* 12: 153-162.
- Ritchie J.M. 1981.** A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae). *Bulletin of the British Museum (Natural History)* 43: 83-183.
- Ritchie J.M. 1983.** Determination of sex and instar number of nymphs of the senegalese grasshopper, *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae). *Entomologist's Monthly Magazine* 119: 97-101.
- Saraiva A.C. 1962.** Plague locusts *Oedaleus senegalensis* and *Schistocerca gregaria* in the Cape Verde Islands. *Estudios agronomicos* 3: 61-89.
- Schaeffer G.W. 1976.** Radar observations on insect flight. *Symposia of the Royal entomological Society of London* 7: 157-197.
- Shah P.A., Godonou I., Gbonghoui C., Hossou A., Lomer C.J. 1998.** Survival and mortality of grasshopper egg pods in semi-arid cereal cropping areas of northern Benin. *Bulletin of Entomological Research* 88: 451-459.
- Shah P.A., Godonou I., Gbongbou C., Hossou A., Lomer C.J. 2000.** Enumerative sampling plans for grasshopper egg pods in northern Benin. *Journal of Applied Entomology* 124: 391-394.
- Sidibe B. 1998.** Le problème acridien au sahel. *Agrhymet Info, Niamey, Niger* 3: 6-10.
- Singh S., Bhatia D.R. 1965.** Gregarization of low density desert locust hopper populations as a result of association with other grasshoppers. *Plant Protection Bulletin* 17: 1-2, 7-9.
- Southwood T.R.E. 1977.** Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337-365.
- Stonehouse J.M., Gbongbou C., de Groot A., Lomer C., Ly S., Maiga I., Tijani, 1997.** Grasshopper control in the Sahel: farmer perceptions and participation. *Crop Protection* 16: 733-741.
- Tappan G.G., Moore D.G., Knusenberger W.I. 1991.** Monitoring grasshopper and locust habitats in Sahelian Africa using GIS and remote sensing technology. *International Journal of Geographical Information Systems* 5: 123-135.
- Tappan G.G., Tyler D., Moore D.G. 1990.** Seasonal vegetation mapping by satellite for grasshopper and locust control in Africa, p. 69-72 in: **U.S. Geological Survey (ed.),** *United States Geological Survey Yearbook: Fiscal Year 1989.* U.S. Geological Survey, Reston, VA, USA.
- Tappan G.G., Moore D.G. 1989.** Seasonal Vegetation Monitoring with AVHRR Data for Grasshopper and Locust Control in West Africa, p. 221-234 in: *Proceedings, International Symposium on Remote Sensing of Environment, 22nd, Abidjan, Cote D'Ivoire, October 1988, Vol. 1.*
- Taylor L.R. 1986.** The four kinds of migration, p. 265-280 in: **Danthanarayana W. (ed.),** *Insect flight: dispersal and migration.* Springer-Verlag, Berlin.
- Traore S., Sidibe B., Djaby B., Samba A., Kaba A.B., Sarr B., Amani A., Some B., Andigue J. 2004.** A review of agrometeorological monitoring tools and methods used in the West African Sahel, p. 209-220 in: **Motha R., Sivakumar M.V.K., Bernardi M. (eds.),** *Strengthening Operational Agrometeorological Services at the National Level.* Proceedings of a Inter-Regional Workshop held 22-26 March 2004 in Manila, Philippines. AGM-9, WMO/TD-No.1277. World Meteorological Organization, Geneva, Switzerland.
- Tucker C.J., Hielkema J.U., Roffey J. 1985.** The potential of satellite remote sensing of ecological conditions for desert locust survey and forecasting. *International Journal of Remote Sensing* 6:127-138.
- Van Der Valk H., Niassy A. 1998.** Effets de la lutte contre les sauteriaux avec le Fénitrothion sur la mortalité naturelle des oothèques au Sénégal, p. 61-75 in: *Effet de la lutte antiacridienne sur l'environnement Tome II.* FAO, Rome.
- Van der Valk, H., Niassy A., Bèye A.B. 1999.** Does grasshopper control create grasshopper problems? Monitoring side-effects of fenitrothion applications in the western Sahel. *Crop Protection* 18: 139-149.
- Venkatesh M.V., Ahluwalia P.J.S., Harjai S.C. 1972.** Influence of rainfall on the egg diapause of *Oedaleus senegalensis*. *Plant Protection Bulletin* 23: 20-27.
- Yonli O.T. 1990.** Parasitisme des oothèques de sauteriaux au Mali. *Sahel PV Info* 23: 3-5.