CROP PROTECTION PROGRAMME

Development of an outbreak forecasting tool for the Senegalese grasshopper*, Oedaleus senegalensis,* using satellite and ecological data

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FINAL TECHNICAL REPORT

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Executive Summary

The project's purpose was to investigate the relationships between remote-sensed, environmental factors and the biology of both the Senegalese grasshopper, *Oedaleus senegalensis*, and its predators, in order to develop a population model for this pest species. Apart from its value in providing an improved understanding of the mechanisms that cause *O. senegalensis* outbreaks, the model's importance lies in its potential role as a decision-making and forecasting tool for predicting major outbreaks of this pest in the sahelian zone of West Africa.

The research activities and outputs were as follows. Field surveys were carried out in Northern Cameroon and data on the composition of the *O. senegalensis* predator complex were collected. The Southern limits of the *O. senegalensis* habitat in Cameroon were also delineated during these surveys. Remote-sensed thermal infrared data, that can be used to estimate spatial and temporal patterns of rainfall, were obtained and analysed for the *O. senegalensis* habitat. This was used to devise a classification of rainfall season types, and in turn, season type determines *O. senegalensis* population dynamics and movement. Data on the *O. senegalensis* population and on the location of outbreaks during the period 1989-1997 were obtained through a literature search and from the 'Centre Regional AGRHYMET' series of publications. The *O. senegalensis* population model was built to contain parameters for migration, diapause, predation and environmental factors. The performance of the model was assessed using both historical and current information on *O. senegalensis* population dynamics and environmental factors. The best fit to the *O. senegalensis* population data was obtained when both the habitat suitability for the predators and the weather (season type) were longitudinal-zone specific. In particular, a period of severe outbreaks that occurred between longitudes 0 and 20E in the years 1995-97 was predicted by the model. This provides a rational way of synthesising environmental and biological data for informed forecasts of *O. senegalensis* pest pressure. It is also an innovative tool that can aid decision-making when resources are limited. The model can generate forecasts for target countries (Cameroon and Nigeria) as well as for other areas, which would be of use to international donor bodies and National Plant Protection Departments (NPPDs). The project's research and model were promoted through a visit to the Locust and Grasshopper group at PRIFAS/CIRAD, Montpellier, where appropriate forecast uptake pathways were discussed. Results were also disseminated through the publication of peer-reviewed papers. These

outputs have contributed to the project goal by creating a tool that enables forecasts of *O. senegalensis* pest pressure to be made and thus could reduce the impact of this migrant pest on crop production in the Sahel through the use of more timely control interventions.

Background

The Senegalese grasshopper, *Oedaleus senegalensis* (Krauss), is arguably the most serious grasshopper pest of millet and other subsistence crops in the sahelian zone of West Africa. Severe outbreaks occurred in 1985, 1986 and 1989 (Cheke, 1990), but possibly the worst on record occurred in 1974 when *O. senegalensis* infested 3.5 x 10^6 ha, resulting in the loss of 368,000 tonnes of agricultural production (Bernardi, 1986). Donor assistance for control operations during this outbreak alone amounted to over US$ 5 million (Popov, 1988).

The ODA Locust Strategy recommended a move away from emergency aid to one in which the emphasis is on preparedness and prevention. It recognised that research is needed if new approaches to locust and grasshopper forecasting and control are to be found. Improved forecasting should enable national and international teams to improve the efficiency of their control efforts, reduce both crop losses and environmental contamination and control costs. At the time the project proposal was written, the only attempt to forecast *O. senegalensis* pest pressure had been a biomodel run by CIRAD/PRIFAS, which did not include critical biological processes such as diapause and predation (see Cheke (1990) for a critique).

Demand for improved forecasting tools clearly exists and was expressed by National Plant Protection Department (NPPD) staff at the International Conference on New Strategies in Locust Control, Bamako, April 1995. An advisory report to the CPP also suggested the need to develop insect-population models that improve outbreak predictions for migratory pests. In addition, under the RNRRS at that time, problems caused by *O. senegalensis* in the Semi-arid Production System had been identified as targets for research. National programme staff in Cameroon (IRAD, Garoua Station), for whom *O. senegalensis* is periodically a serious problem, had also expressed a strong interest in this line of research.

One of the problems faced by National Plant Protection Departments (NPPDs), when deciding how to allocate scarce resources for effective early season control, is the difficulty in obtaining rainfall data rapidly from remote sites. These data can be used as an indicator of the timing of the emergence of the *O. senegalensis* population (Burt *et al.*, 1995). Remote sensing of rainfall by satellite can help solve this problem and aid in decision making when resources for control are scarce (Burt *et al.*, 1995). This has several important limitations, however, in that it cannot predict damage caused by migrant *O. senegalensis*, the forecasts are very short-term (10 - 12 days) and it cannot predict the build-up of the *O. senegalensis* population as the rainy season progresses.

In order to overcome these limitations, it was necessary to understand how the *O. senegalensis* outbreak mechanism(s) operates. To this end, two population models have been built (Colvin & Holt, 1996; Holt & Colvin, 1997) to examine quantitatively, the complex relationships between *O. senegalensis* migration, diapause, egg-pod predation and rainfall (Saraiva, 1962; Fishpool & Cheke, 1983; Riley & Reynolds 1983; Colvin & Cooter, 1995; Colvin, 1996). The first model examined the dynamics of an age-structured grasshopper population, but had no spatial component (Colvin & Holt, 1996). The second, which was completed during the lifetime of this project, considered migration processes between zones of the Sahel, but was a general model suitable only for investigating some of the principles underlying *O. senegalensis* outbreak dynamics (Holt & Colvin, 1997). Both models highlighted the importance of egg predation in the prevention of outbreaks and indicated that it is when this natural regulatory mechanism breaks down, possibly during prolonged periods of drought, that the risk of subsequent outbreaks is highest. These models also revealed important gaps in our knowledge of the system and the ecological activities of this project were intended, in part, to obtain this additional information.

The models also highlighted the importance of rainfall patterns and the movements of the Inter-Tropical Convergence Zone (ITCZ) in the generation of outbreaks. Information on rainfall patterns in time and space, and the resulting changes in vegetation, are available from satellite remote-sensed data. Vegetation change over the course of the rainy season may be assessed from Normalised Difference Vegetation Indices (NDVIs) prepared from Advanced Very High Resolution Radiometer (AVHRR) images.

Building on previous work, it was proposed to utilise both recent and historical satellite data, combined with information on the biology and ecology of *O. senegalensis* and its predators, to build a forecasting and decision-making tool that would predict *O. senegalensis* pest pressure for regions of the Sahel.

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Project Purpose

Purpose 4, Output 1 **-** Population and behaviour models of economically important locust, grasshopper and armyworm outbreaks developed and improved pest-control strategies promoted.

Indicative output 4.1.2 **-** Develop models to improve grasshopper forecasting and management.

Investigations to establish the interactions and relationships between environmental factors and the biology of *O. senegalensis,* in order to develop a decision-making and forecasting tool for predicting outbreaks of this pest in the Sahel.

Research Activities

Ecology and Biology

***Activity 1a*. *Field surveys for egg-pod predators*.** Information on the relative importance of *O. senegalensis* egg-predator species in the Southern regions of its habitat is scarce and therefore monthly egg-pod surveys in the Cameroon were planned to collect these data. It was planned that the equipment for this activity, such a mist-blower to uncover the tops of the egg pods, would be purchased in the Cameroon by the IRAD staff. In the wet season, surveys were also planned to assess the abundance of *O. senegalensis* adults and hoppers.

Activity 1b. Fecundity and adult feeding requirements of egg-pod predators. The ecology and biology of important egg-predator species such as the flies, *Xeramoeba oophaga* and *Systoechus* spp., and the beetles, *Mylabris* spp., is poorly understood. Experiments were planned, therefore, to determine the fecundity, adult feeding requirements and survival under drought conditions of key species in order to provide parameter estimates for the model (IRAD activities). Accurate information on egg predators was required because the existing models indicated that poor predator survival during droughts is probably a significant factor contributing to the upsurge in grasshopper numbers when ‘good’ conditions return. The following methodologies and activities were proposed:

*Field estimates of egg-pod mortality***.** To assess the relationship between egg-pod density and predation, bi-monthly egg-pod surveys were planned according to the following methodology. Ten sites of ca. 500 m^2 will be sampled per survey and five randomly selected 4 m^2 areas per site will be searched for egg pods. The numbers of ‘surviving’ and predated egg pods, as well as the predator species responsible for the mortality will be recorded. Data were to be analysed as an ANCOVA with binomial errors. This would have told us whether egg-pod predation is density independent or not in the Cameroon and therefore the extent to which the egg predators are likely to constrain *O. senegalensis* in this region (IRAD & NRI in years 2 - 4).

Collection and identification of the primary egg-predators in the Cameroon. It was planned to obtain larvae of the principal egg-pod predators, e.g. *Xeramoeba oophaga*, *Systoechus* spp. and *Mylabris vicinalis*, during the egg-pod surveys. Larvae were to be maintained in the laboratory and the emerged adults identified and used for experimentation. Specimens of *X. oophaga* and *M. vicinalis* are available at NRI and were to be provided to the IAR to assist identification. Species not encountered in the previous fieldwork in Mali, e.g. *Systoechus*, were to be sent to the Natural History Museum for identification. If numbers of predators obtained from the surveys were low, alternative ways of collecting them would have been tried, e.g. *M. vicinalis* can be caught in light traps, particularly during the period when millet is flowering (IAR & NRI in years 2 - 4).

*Timing of predation throughout the year***.** A culture of *O. senegalensis* was to be maintained in the laboratory at the IRAD and diapausing egg pods obtained from it. At bi-monthly intervals, one hundred egg pods were to have been placed into a purpose-built sand pit. These were then to have been dug up after two months and dissected to determine mortality due to predation (IAR & NRI in years 2 - 4).

Nymphal mortality in the wet season. Numbers of *O. senegalensis* nymphs emerging after the first rains of the wet season were to have been assessed by sampling transects using a sweep net. The transects were to have been sampled two and four weeks later to obtain estimates of nymphal mortality. If sufficient numbers of *O. senegalensis* remained in the area for a second generation, the procedure would have been repeated (IAR & NRI in years 2 - 4).

Laboratory assessment of predator parameter estimates.

M.v. *Adult diet and fecundity* - *M. vicinalis* adults were to be provided with flowering millet and sorghum heads for food (Doumbia, 1992). Meloinae eggs are usually laid in batches at depths of 1 - 2.5 cm in moist sand (Selander, 1981). Eggs from individual, mated, fed females were to be collected and counted to assess fecundity (IAR years 2 & 3).

Survival under drought conditions – It was planned to assess the fecundity of starved *M. vicinalis* females. Field collected *M. vicinalis* larvae were to be maintained individually in small test tubes in the lab. to determine whether this species has a diapause and, if so, how long it lasts (a diapause strategy may allow the predator species to survive periods of adverse environmental conditions). Triungulin (*M. vicinalis*) larvae were to be maintained in wet and dry sand to assess their longevity in the absence of egg pods (IAR years 2 & 3).

X.o. *Adult diet and fecundity* - Adult *X. oophaga* were to be provided with sugar solution (10% w/v) on emergence to assess whether the availability of nectar might be important to this species (sugar solution provides an acceptable substitute to nectar for other insects, e.g. noctuids). Nothing was known about how and where *X. oophaga* oviposits and therefore adult *X. oophaga* were to be released into a netting cage where the floor consisted of a sand-filled tray containing *O. senegalensis* egg pods positioned vertically in the sand with their tops level with the sand surface. Behavioural observations were to confirm whether adult females locate the egg pods before oviposition or whether their host location strategy is similar to that of *M. vicinalis* where the triungulin larvae move through the soil and locate the egg pods (IAR years 2 & 3).

Survival under drought conditions - As for *M. vicinalis* above.

S. spp. *Adult diet and fecundity* - As for *X. oophaga* above.

Survival under drought conditions - As for *X. oophaga* above.

For these sets of activities, necessary equipment for IRAD included a mist blower and a laptop computer with e-mail link for data management and facilitation of cheap, rapid communication between IRAD and NRI.

In order for the IRAD project staff to carry out the above work (activities 1a & 1b), it was necessary for them to purchase a mist-blower and to have grasshopper cages constructed. Funds for this were sent to IRAD but due to a financial irregularity there the equipment was never purchased. The facts of the situation were explained to NRInternational by NRI staff and NRInternational terminated the contract with IRAD shortly afterwards. Subsequent to this, a new Chief of Station at IRAD wrote to say that he was unable to say what had happened to the funds. NRInternational agreed that the NRI/Oxford component of the project could continue and activity 1 was modified to:

Modified Activity 1. Information on the relative importance of *O. senegalensis* egg-predator species and other causes of mortality will be obtained, as far as possible, from the literature. This will involve obtaining a complete set of PRIFAS & AGRHYMET-CILSS publications containing references to *O. senegalensis* biology and ecology (NRI, year 2).

Satellite and O. senegalensis outbreak data

Activity 2a. **Satellite data.** In the initial part of the project, field surveys were to be carried out in the Cameroon to determine the Southern limit of the *O. senegalensis* habitat to facilitate interpretation of the satellite data. It was assumed that this process would be aided by the polyphagous nature of *O. senegalensis*, which would probably avoid the need to distinguish individual plant types. Rainfall data, necessary for ground truthing the satellite images were to be provided by IRAD, Cameroon. Satellite data, for 10 day intervals, were to be provided by the TALA Research Group, Oxford. They were also to provide the programming expertise necessary to manipulate the data into a format suitable for input into the model.

Activity 2b. O. senegalensis outbreaks. It was planned to carry out at literature search to obtain information on all recorded *O. senegalensis* outbreaks with particular emphasis on the period (1982 to 1987).

Modelling and forecasting

Activity 3a. **Model building.** Previous conceptual and simulation models of *O. senegalensis* outbreak mechanisms divided the *O. senegalensis* habitat into different latitudinal zones (Popov, 1988; Launois, 1978; Holt and Colvin, 1996). We also proposed to divide the *O. senegalensis* west African habitat into defined longitudinal zones (of which the Lake Tchad region will be one), in each of which a modification of the Colvin and Holt (1996) model was to be run. This model currently included information on diapause duration, predation and environmental factors. Latitudinal zones in the new model were to be connected by migration based on the timing and movements of the ITCZ, inferred from satellite data. Biological data on predators collected during the project were to be used to provide realistic parameter estimates for the model (NRI).

Activity 3b. Model validation using historical data. During the period between 1981 and 1991, the Sahel experienced three major *O. senegalensis* outbreaks. The TALA research group will provide processed historical satellite data on key environmental factors such as vegetation growth in space and time. Rainfall estimates are also available from published climatological data. These data were to be used to run the model to see if a realistic pattern of outbreaks can be generated.

Activity 3c. Forecasting and validation using current data. If the model proves successful in 3b, it was to be run using current satellite data as an outbreak-risk assessment tool for the different zones, based on the possible range of future environmental conditions, and its performance assessed. During the lifetime of this project, therefore, it was planned that NRI staff would run the model. Once the model had been validated successfully, forecasts could be made available to West African NPPDs and the Commission de Bassin du lac Tchad, either directly or through the fortnightly Surveillance Des Acridiens Au Sahel newsletter (NRI).

Activity 3d. Project promotion. Contact West African National Plant Protection Departments, CIRAD and the FAO to keep them informed of progress (NRI, years 2, 3 and 4).

Activity 4. Publications. Production of at least one peer-reviewed scientific publication (NRI, Oxford, years 3 and 4) and dissemination of results through visits to CIRAD and presentations at international conferences (NRI, years 3 & 4).

All the above research activities were carried out as planned and apart from the presentation of the model at an international conference, the outputs were achieved.

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Outputs

Output 1. Key information on the composition of the O. senegalensis predator complex available.

Prior to the termination of the IRAD contract, three field surveys were conducted and limited data were obtained on the *O. senegalensis* egg-pod predators (Tables 1 & 2), as well as other causes of *O. senegalensis* mortality in the Cameroon. The available data indicate that a high proportion of the mortality has already occurred by the end of the rains in October. In addition, and of particular note, was the high level of adult mortality in field collected insects, probably due to the presence of parasitic worms, which were found in the thoracic cavity and abdomen of dead adults.

Larvae of egg-pod predators, collected during the egg-pod surveys and from purpose-built sandpits, were maintained in the laboratory and the adults that emerged were identified. These included *X. oophaga* and *Mylabris* spp., as well as fly species that IRAD staff could not identify.

A literature search was carried out and relevant publications obtained. In addition, approximately 20 publications containing relevant information on *O. senegalensis* biology and ecology were obtained from CIRAD/PRIFAS & AGRHYMET-CILSS.

Output 2a. Data relating to spatial and temporal patterns of rainfall obtained for O. senegalensis throughout its range.

Rainfall data for the western Sahel, expressed as % departures from the 1951-80 average, were obtained from the Climatic Research Unit, University of East Anglia, for the period 1907-1990. From 1989, satellite derived rainfall information is available and this was obtained and processed by the TALA group, University of Oxford.

Season classification using CCD images

O. senegalensis reproduction and movement has been described in relation to three ecological zones: Northern, Middle and Southern, previously called the ASM, ATM and AMI, respectively (Launois, 1979). These were based on both rainfall and *O. senegalensis* sampling data and occur geographically as three latitude bands, which extend across the *O. senegalensis* habitat.

Work of the TAMSAT program (Univ. of Reading) showed that cold cloud duration (CCD) values correlate with rainfall in the region of interest in West Africa (Grime, *et al.* 1992). Approximately 10 mm of rainfall is sufficient to cause *O. senegalensis* emergence after 10-14 days (Burt *et al*., 1995) and therefore it was decided to use CCD data to drive the model rather than NDVIs or Soil Adjusted Vegetation Indices (SAVIs). Using the long-term mean CCD values, a good correspondence was achieved with the *O. senegalensis* ecological zones and a classification based on the CCD images was used to redefine the boundaries of these zones. Thirteen CCD zones (termed rainfall zones) were conveniently distinguished North to South across the *O. senegalensis* habitat and also spanning the geographical distribution of recorded outbreaks between 1972 and 1980 (Popov, 1988) (Figure 1). Rainfall zones 4 - 5, 6 - 10 and 11 - 13 corresponded approximately to the Northern, Middle and Southern zones, respectively (Figure 1).

The mean CCD value was calculated for each of the cells of a geographical grid formed by the intersection of the 13 rainfall zones with 10 longitudinal zones, each 5 degrees wide and extending from -20 degrees (20 degrees West) to +30 degrees (30 degrees East). For some purposes mean values were calculated for the three redefined ecological zones whilst for others, the thirteen rainfall zones were treated separately. Grid cell means were calculated for a sequence of 108 monthly images during the eight-year period from 1989 - 1997. It was possible, therefore, to examine differences in rainfall pattern both longitudinally across the *O. senegalensis* habitat, and from year to year. Figure 2 shows an example comparing the variation in CCD over a twelve-month period in the three ecological zones.

The CCD values in May/June and in October proved useful in distinguishing differences in rainfall profile between years. The following criteria were used to determine season type in each year. The CCD cell values were compared with the 9-year average for the same cell and month. The rains were classed as having an early start in the Southern and the Middle zone if the value for May was greater than the 9-year average, and in the North if the value for June was greater than the 9-year average. This adjustment was necessary due to the later start of the rainy season in the Northern zone. Otherwise, the rains were deemed to start late. The rains were classed (for all zones) as retreating late if the value for October was higher than the 9-year average. Otherwise the retreat was deemed early. The sum of the CCD values for all the months of a year were compared with the 9-year mean. If the value of a particular year was higher or lower than the mean, then that year was classified as wet or dry, respectively. An example of annual CCD curves and their classification is shown in Figure 3.

A gradual Southerly movement of the ITCZ in the autumn is associated with a steady retreat of the rains. When the ITCZ does not show this pattern, the rains tend to peter out throughout the region in a rather unstructured way and this was termed stagnation by Popov (1988). This has implications for the *O. senegalensis* population dynamics and was considered important in the development of outbreaks by Popov (1988).

Rainfall less than 10 - 20 mm per month, which is approximately equivalent to 5 h CCD (Grimes *et al.*, 1992), is insufficient for *O. senegalensis* to breed effectively. We determined the month in which the rains declined below this threshold across the 13 rainfall zones. In a year with gradual retreat of the rains, the expected pattern is shown in Fig. 4a. In contrast, a stagnation pattern is shown in Fig. 4b, in which the rains dissipate throughout the region without showing a Southward progression over time.

Using the CCD data, therefore, seasons were classified as being wet or dry, with an early or late start, and a retreat which is either early, late or a stagnation. By applying the above criteria, it was possible to classify the seasons into twelve (2x2x3) types, which were given a unique identifying number:

1. Early, dry, early.
2. Early, dry, late.
3. Early, dry, stagnate.
4. Early, wet, early.
5. Early, wet, late.
6. Early, wet, stagnate.
7. Late, dry, early.
8. Late, dry, late.
9. Late, dry, stagnate.
10. Late, wet, early.
11. Late, wet, late.
12. Late, wet, stagnate.

Output 2b. Data on previous O. senegalensis outbreaks collected through a literature search.

Information on *O. senegalensis* outbreaks going back to 1949 was collected through a literature search. More detailed and location specific data on *O. senegalensis* populations is sent to the regional centre of AGRHYMET, Niamey, by the National Plant Protection Departments of Mauritania, Cape Verde, Senegal, Gambia, Niger, Mali, Burkina Faso, Guinee-Bissau and Tchad. This information is then included in AGRHYMET's regional synthesis called "Situations Agrometeorologique et Hydrologique Dans Les Pays Du CILSS". They also publish a monthly bulletin called "Special AGRHYMET" which contains more detailed reports of pest problems in these Sahelian countries. Back editions of these publications, as well as FAO reports, were obtained from AGRHYMET and an *O. senegalensis* outbreak data set starting from the pan-sahelian outbreak in 1989 was generated from them. The reports on the *O. senegalensis* population were summarised in the following way. For each month of the growing season, a score was given to each country according to the severity of the damage caused by *O. senegalensis*, i.e. no damage reported and *O. senegalensis* densities of 0-5 m^{-2} was given a score of 0. Isolated areas of damage and/or *O. senegalensis* densities of 6-29 m^{-2} was awarded a score of 1. Severe or widespread damage and/or *O. senegalensis* densities of more than 30 m^{-2} was given a score of 2. Where no data were available, a missing value was recorded. The mean value for the *O. senegalensis* population in a year, in a longitudinal strip, was obtained, from the average of the monthly scores for that year, for all the countries that fell within the longitudinal strip. The data are shown graphically in Figure 5.

Output 3a. An O. senegalensis population model including parameters for migration, diapause, predation and environmental factors.

Where a mixture of qualitative and quantitative data exist, rule-based simulation provides an approach to model building that utilises directly the different data types (Starfield and Bleloch, 1986; Holt and Day 1993; Holt and Cheke, 1997; Holt, Tucker, Mushobozi and Venn, 1999). In this case, the principal of parsimony was adopted to build a model that contained only those elements of *O. senegalensis* ecology and movement that are crucial to the population processes that lead to outbreaks. The model simplifies the population dynamics and movement of *O. senegalensis* by partitioning the habitat spatially into three ecological zones: Northern, Middle and Southern (N, M & S) and by distinguishing three time periods during the course of each rainy season. In each period, one or more generations of the grasshopper can occur (or indeed none, if the eggs remain quiescent during that period). Transitions between the zones and time periods reflect the range of processes that can occur and depend upon the meteorological conditions prevailing in the season. This 9-node (3-zone x 3-period) structure is the simplest form that allows key features of *O. senegalensis* ecology to be represented. A schematic diagram of the model (Figure 6) shows the transitions that occur and the parameters associated with each.

Transition rates between nodes depend on parameters denoting, with subscripts appropriate for each transition i, or zone Z, the growth of the population, r_i, the proportions of individuals migrating, a_i, and the losses due to predators, P_Z. Other causes of mortality such as poor food quality are incorporated in the value of r_i. Quantitative estimates of each parameter were not feasible, but based on information derived from published research (e.g. Popov 1980, 1988; Launois 1979), it was possible to judge whether the value of a parameter would be expected to increase or decrease under the different meteorological conditions prevailing in a particular season. These judgements were collated and structured by simplifying the description of the meteorological conditions to a small set of discrete season types.

Table 3 summarises the judgements made about the relative values of each of the parameters under the different season types. These judgements can be regarded as a set of rules that relate *O. senegalensis* population dynamics to rainfall patterns. Parameter values were defined on an ordinal scale. In the case of r, an eight-point scale from 'large decrease' to 'very large increase' was used, and for P a 7 point scale from 'large decrease' to 'large increase'. To encompass an appropriate range of variability of r and P, the scale points were regarded as logarithmic rather than linear, e.g. the sequence: small, moderate, large, very large, represented the series: e^{n}, e^{n+1}, e^{n+2}, e^{n+3}. To categorise m, a four-point scale ('none', 'few', 'moderate', 'most') was used, which was taken to correspond to 0, 10%, 80% and 99%, respectively.

The approach formalises a qualitative understanding of the biological processes in a format that could be used to build a model. The description of the parameter values is deliberately both relative and qualitative. This format best utilised the variety of information available in the literature. An iterative process, with the constraint that their number did not exceed the resolution of our understanding, determined the number of scale points. An initial three-point scale was used in all cases, and resolution was increased only when needed to reflect perceived differences between season types. Appendix 1 summarises the reasoning and assumptions pertaining to each season type. These led to the set of judgements expressed as rules (Appendix 2), which are summarised in Table 3.

Model specification

The population is modelled on a logarithmic scale and therefore sums rather than products specify changes. Where populations are split or combined, however, as happens when movement between zones occurs, the terms are necessarily handled as exponents. The numbers in each node (Fig. 6) are specified as follows.

$$N_1 = \mathrm{Ln}\left(1 - a_4 - a_5\right) + N_3 + r_{14} - P_N \qquad \text{eqn 1}$$

$$M_1 = \mathrm{Ln}\left[a_5 \mathrm{Exp}\left(N_3 + r_{13} - P_N\right) + \left(1 - a_3\right)\mathrm{Exp}\left(M_3 + r_{12} - P_M\right)\right] \qquad \text{eqn 2}$$

$$M_1 = \mathrm{Ln}\left[a_4 \mathrm{Exp}\left(N_3 + r_{11} - P_N\right) + a_3 \mathrm{Exp}\left(M_3 + r_{10} - P_M\right) + \mathrm{Exp}\left(S_3 + r_9 - P_S\right)\right] \text{eqn 3}$$

$$N_2 = N_1 + r_4 + P_N \qquad \text{eqn 4}$$

$$M_2 = \mathrm{Ln}\left[\mathrm{Exp}\left(M_1 + r_3 - P_M\right) + a_1 \mathrm{Exp}\left(S_1 + r_2 - P_S\right)\right] \qquad \text{eqn 6}$$

$$S_2 = \mathrm{Ln}\left(1 - a_1\right) + S_1 + r_1 - P_S \qquad \text{eqn 5}$$

$$N_3 = \mathrm{Ln}\left[\mathrm{Exp}\left(N_2 + r_8 - P_N\right) + a_2 \mathrm{Exp}\left(M_2 + r_7 - P_M\right)\right] \qquad \text{eqn 7}$$

$$M_3 = \mathrm{Ln}\left(1 - a_2\right) + M_2 + r_6 - P_M \qquad \text{eqn 8}$$

$$S_3 = S_2 + r_5 + P_S$$

where,

N_i, M_i and S_i (ln number) are the abundance's of *O. senegalensis* in the Northern, Middle and Southern zones, respectively, in period i,
r_1, r_2 .... r_{14} (ln number) are the population changes associated with each transition,
a_1, a_2 .... a_5 are the proportions of the population making the transitions,
P_N, P_M and P_S (ln number) are the moralities due to predation in each zone.

The model is not age structured and so, in order to write a set of difference equations, a 'census point' was taken which related one period to the next that was the numbers of eggs counted just after oviposition. For example, S_1 is the size of the egg population just after oviposition by adults that emerged at the end of period three. The increase terms r_i refer to the change in population size from eggs at the end of one period to eggs at the end of the next. For example, r_1 is the change in the population from just after the eggs are laid in the Southern zone by adults from period three to the laying of eggs by adults emerging and laying in the Southern zone at the end of period one. The migration terms a_j specify the proportions of the population redistributed between zones. For example a_1 is the proportion of individuals that emerge from eggs at the beginning of the season in the Southern zone that migrate (as adults) to the Middle zone.

Changes in mortality due to predation depend on changes in the success of the predators from season to season. As with *O. senegalensis,* this is largely determined by rainfall. Apart from birds, predatory species that attack *O. senegalensis* are not known to migrate and the mortalities caused by them in each zone in season *t* are given by:

$$p_{N,t} = p_{N,t-1} + v_3 \qquad \text{eqn 9}$$

$$p_{M,t} = p_{M,t-1} + v_2 \qquad \text{eqn 10}$$

$$p_{S,t} = p_{S,t-1} + v_1 \qquad \text{eqn 11}$$

where v_i is the change in population size since the previous year, determined by the previous year's season type.

To retain, as far as possible, a model specified purely in terms of the qualitative judgements summarised in Table 3, constraints to population dynamics were imposed by simple arbitrary limits. Density dependent constraints to population growth do exist, although the form of this may vary (Holt & Colvin, 1997). Bounding the variables as follows imposed the limits:

$$-8 \le N_i, M_i, S_i \qquad \text{eqn 12}$$

$$0 \le P_Z \le 6 \qquad \text{eqn 13}$$

$$-7 \le \mathrm{Ln}(1 - a_4 - a_5) \le 0 \qquad \text{eqn 14}$$

Thus, *O. senegalensis* abundance has a lower bound of e^{-8} (unit area^{-1}) in any zone or period, but there is no upper limit (eqn 12); the mortality due to predators has both upper and lower bounds (eqn 13); and eqn 14 prevents the proportion remaining in N_3 dropping below e^{-7}.

Output 3b. Assessment of model performance using both historical and current information on O. senegalensis population dynamics and environmental factors.

The dynamic behaviour of the model was explored for different sequences of season type within a longitudinal strip. To indicate the kind of output that can occur, three population trajectories are illustrated (Fig. 7a, b and c). The *O. senegalensis* abundance summed over the three periods is shown for each zone. In Fig. 7a, the six types of dry year occur in a repeated sequence. The *O. senegalensis* population remains at a low level but several features can be seen. There is an increase in the North following stagnation conditions (types 3 & 9) in the previous season. Although season type 2 is dry, it is also long and so boosts the population to some extent in the Middle and South. The predators gradually die out, most quickly in the North and less quickly in the South.

In Fig. 7b, the six types of wet year occur in a repeated sequence and the population shows an initial increase. Season type 5 is long and wet and boosts the population everywhere in the following year. This is also long and wet but ends in a stagnation event (type 6), which causes a very large population in the North the following year. With continued wet conditions, predator numbers build up rapidly with those in the Middle and North increasing more quickly than in the South with a resulting collapse in *O. senegalensis* numbers. Although grasshopper numbers have been reduced to a very low level, predators remain high because their survival is determined by environmental conditions. This conclusion may not be too unrealistic because some of the *O. senegalensis* predators, such as ants, are generalists.

In Fig. 7c, a sequence of four dry, two wet and six dry season types is illustrated. The sequence starts as for Fig. 7a, but two wet seasons of adequate length for the grasshoppers to complete their lifecyle and migration cycle successfully cause a very large population, particularly in the Middle zone in the following season.

The results of these and other test sequences were found to be explicable biologically and provided insights that were not apparent beforehand. Some further model testing was carried out by comparing model output with *O. senegalensis* outbreak records available from the literature for the period 1949 to 1990. The outbreak records are incomplete due to deficiencies in reporting; in addition, rainfall data for this period was based on gauges rather than CCD and gave only the annual rainfall departure from the long-term mean, i.e. a measure of wetness. Nevertheless, useful comparisons were possible. A high simulated population in the Northern zone was taken as an indication of high outbreak risk.

In the late 60s and early 70s, prolonged drought occurred in the Sahel. Then in 1974, conditions improved when some rain fell over much of the Sahel. However, a good harvest was not obtained due to grasshopper attack, which devastated crops (Popov, 1988). The sequence of years from 1972 to 1983 saw 4 years in which there were reports of serious *O. senegalensis* outbreaks: 1974, 75, ‘77, ‘78. The sequence started with three very dry years, followed by a wetter year in which there was an outbreak report. This was followed by an average year, two further dry years, and then an average year. Outbreak reports coincided with the second of the two dry years and the wet year (Fig. 8a). In model simulations it was found that higher numbers were predicted in the Northern zone in the wet years. This was critically dependent on the occurrence of stagnation in the previous year. In the absence of stagnation, numbers in the Northern zone did not build up dramatically until the year after the favourable wet conditions. Unfortunately details are lacking as to the pattern of rainfall. It was nevertheless instructive to investigate which patterns can lead to simulated high numbers in seasons when outbreaks were recorded.

In the sequence of years 1940 to 1952, the relationship between wet years and outbreaks was rather different. Again, the sequence started with three dry years followed by a wet year. Outbreaks are not reported in the wet year. This was followed by a dry year and two further wet years. Three dry years then follow and outbreaks were reported in the second and third of these dry years (Fig. 8b). This was consistent with simulation results if stagnation occurred following the two wet years. In this way populations are retained in the North and lead to high simulated populations coinciding with the time of the outbreaks.

A sequence of very wet seasons occurred between 1952 and 1963. Outbreak reports exist from 1955, part way through this sequence (Fig. 8c). As can also be seen in Fig. 7b, good conditions over several years lead in the model to an *O. senegalensis* population peak and collapse. This peak in numbers might be expected to result in outbreak reports.

Comparing model predictions with historical data for the period 1989 to 1997

O. senegalensis population data for the period 1989 to 1997 (AGRHYMET publications) were reviewed and the results summarised by year and longitude strip using a three point scale (see output 2b & Figure 5). For the same nine-year period, season type was also classified for each longitude strip using cold cloud duration (CCD) data, as explained previously (see output 2a). CCD data was not available in an appropriate form prior to this period but simulations were initiated three years earlier based on rainfall records: 1988 was relatively wet and the previous two years, 87 and 86, were relatively dry. For simplicity all longitude strips were initiated with the sequence 7, 7, 5. Simulations were performed over the twelve-year period from 1986 to 1997 for each longitude strip. This gave the outbreak prediction pattern for 1989 to 1997 shown in Figure 9a. None of the original qualitative judgements detailed in Table 3 were changed but the magnitude of the changes were scaled so that the model system rarely encountered its boundary conditions. This was necessary because the judgements detailed in Table 3 concern relative rather than absolute change. Without the scaling, the predators quickly reached the upper boundary and *O. senegalensis* the lower boundary, under most conditions. The scaling used was constant throughout for *O. senegalensis*, but was varied as described later for the predators in order to explore the possibility that predators may be more or less successful in different zones. The scaling takes the form $a(S+b)$, where S is the value in Table 3 and a and b are scaling parameters: a determines the magnitude of the difference between successive scale points and b determines the midpoint value. Unless otherwise stated the scaled values used for *O. senegalensis* and predator population change were $0.5(S+4)$, and $1.5(S-1)$, respectively.

Predators play an important role in the population dynamics of *O. senegalensis* (Colvin & Holt, 1996; Holt & Colvin 1997). Because almost no information is available on variation in *O. senegalensis* predation or predator abundance over the period under consideration, we examined the extent to which the fit of the model might be improved by altering the success of the predators in different parts of the Sahelian zone. This was achieved by altering *b* and for each longitude zone and *b* was optimised to provide the best fit of the model to the data. To understand the impact of this ‘predator fitting’ exercise, simulations were also performed using the longitude-specific values of *b* but with the same sequence of season types for all longitude strips (that for the centre strip, 5). A similar exercise was carried out with the other predator scaling parameter and with the *O. senegalensis* scaling parameters.

Results

The nine-year sequences of season type were found to differ between longitude strips and this gave rise to differences in outbreak predictions for different parts of the Sahelian zone. Figure 9a shows the predictions of the model across the Sahel when no variation in predator success was admitted. The model correctly predicted the upsurge in 1995/6 (Figure 5) but the position of the outbreaks was incorrect, with the model over-predicting outbreaks in the west and under-predicting in parts of the east. The pan-sahelian outbreak at the start of the simulation in 1989/90 was correctly predicted, as was, for the most part, the recession from 1991 to 1994.

The outbreak prediction obtained when the predator scaling parameter was optimised for each longitude strip (Fig. 9b), was much improved over that with a constant value of *b* (Fig. 9a). The effect on predicted outbreaks of varying predator scaling only (Fig. 9b), illustrates that variation in predators alone cannot explain *O. senegalensis* outbreaks. The values of *b* were -0.4, 0.1, 0.5, -1, -1, -0.8, -1.5, -1.4, and -1.3, for zones 1 to 9, respectively.

The preponderance of higher values in the west when predator success is fixed (Figure 9a), indicates that more successful predators must be postulated in this region in order to obtain a good fit to the outbreak reports. Indeed in the absence of the season sequences actually occurring in the west, this led to the collapse of the *O. senegalensis* population, due to predation (Fig. 9b).

When both the weather (season-type sequence) and the predator success parameter were allowed to vary, a good fit to the *O. senegalensis* population data (Figure 5) were obtained (Figure 9c). In particular, the geographical details of the 1995/1996 outbreak were largely correct. This was not a pan-Sahelian outbreak and the differences in outbreak risk predicted by the model for different longitude zones was remarkably similar to outbreak reports for these zones.

Attempts to improve the fit of the model by optimising the other scaling parameters were unsuccessful, supporting the proposition that predator success is critical and variable. We offer a tentative conclusion that a likely source of error in *O. senegalensis* outbreak prediction is lack of knowledge about the *O. senegalensis* predators. The considerable over-prediction of *O. senegalensis* outbreaks in the west in the 1994 to 1997 period when the (Fig. 9a) may reflect an underestimation of the effects on the predators of conditions which also favour *O. senegalensis* increase.

Output 3c. Forecasting and decision tool available for predicting O. senegalensis pest pressure for different Sahelian zones.

The model's output has been compared with *O. senegalensis* outbreak data since 1949 and compared in detail for a nine-year period between 1989 and 1997. When both the weather (season type) and the predators are longitude specific in the model, the fit between the model output and the *O. senegalensis* data is good (Figure 9c). This suggests that the model could be used successfully as a forecasting and decision-making tool. The nine-year validation period is relatively short and a comparison of the model's output with *O. senegalensis* population data over a longer period would increase confidence in the model's performance. As mentioned in the project memorandum, a further phase to the project would also be required to develop a software package to make the model directly usable by non-specialists, necessary if NPPDs or international bodies express a wish to produce forecasts for themselves.

Output 3d. Research and outbreak forecasting tool promoted and results presented at an international conference.

Dr Lecoq and his group of researchers at PRIFAS/CIRAD, Montpellier, were contacted and a visit by Drs Colvin, Holt and Grilli took place between 13-15 October (milestone for Q3) to discuss both the CIRAD *O. senegalensis* biomodel, the NRI forecasting model and appropriate uptake pathways. This visit turned out to be particularly opportune as the CIRAD group were in the process of submitting a joint proposal with AGRHYMET, Niamey, to the World Bank, titled "Integrated approach to solving the problems posed by *Oedaleus senegalensis* and other Sahelian grasshopper pests involving improved outbreak forecasting and optimisation of control strategies". If this proposal is funded, CIRAD agreed it could provide a route through which this project's outbreak forecasts could be disseminated.

No international conferences on grasshopper and locust control, at which to present the forecasting model, were held in the period 1/4/99 – 29/2/00 and so this objective was not achieved.

Output 4. At least one publication produced in a peer-reviewed scientific journal.

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**, 185-103.

Holt, J., Colvin, J., Grilli, M.P. & Rogers D.J. Driving population models with remote-sensed data: an approach to *Oedaleus senegalensis* outbreak forecasting in sub-Saharan Africa. In prep. (a manuscript has been completed and when comments have been received from collaborators it will be sent to a journal by June 2000).

Contribution of Outputs

How the outputs contribute towards DFID's developmental goals?

The project's outputs include a rule-based model for predicting large-scale *O. senegalensis* outbreaks. It has therefore partially addressed the Crop Protection Programme Purpose Output 4.1, "Population and behaviour models of economically important locust, grasshopper and armyworm outbreaks developed and improved pest-control strategies promoted". At the time the project was funded, the DFID (then ODA) Locust Strategy recommended a move away from emergency aid to one in which the emphasis was on preparedness and prevention, recognising that research was needed if new approaches to locust and grasshopper forecasting and control were to be found. The improved ability to forecast outbreaks of *O. senegalensis* should enable national and international teams to improve the efficiency of their control efforts, reduce both crop losses and environmental contamination and control costs. This should in turn contribute to the Purpose of the Semi-arid Production System that was, "Impact of migrant pests on crop production minimised".

The identified promotion pathways to target institutions and beneficiaries.

During the course of the project, it became clear that the most appropriate target institution for the outputs of the project would be AGRHYMET, Niamey. This institute currently publishes a bulletin on the rainfall and agricultural conditions in countries affected by *O. senegalensis*. The bulletin also contains information about damage caused by *O. senegalensis* and it could be expanded to contain forecasts generated by the model.

As part of the project activity to identify promotion pathways to target institutions and beneficiaries, Dr Lecoq and his group of researchers at PRIFAS/CIRAD, Montpellier, were contacted and a visit took place to discuss both the CIRAD biomodel, the NRI forecasting model and appropriate forecast uptake pathways. Dr Lecoq informed us during the course of the visit that PRIFAS/CIRAD were undergoing a restructuring exercise that involved budget cuts. As part of this process, their bulletin “Surveillance des Acridiens au Sahel”, which contained a section for *O. senegalensis* forecasts, was discontinued. This uptake pathway therefore is no longer available. This visit, however, turned out to be particularly opportune as the CIRAD group were in the process of submitting a joint proposal with AGRHYMET, Niamey, titled “Integrated approach to solving the problems posed by *Oedaleus senegalensis* and other Sahelian grasshopper pests involving improved outbreak forecasting and optimisation of control strategies”. This proposal is still going through a lengthy approval process and, if funded, CIRAD agreed it could provide a route through which this project’s outbreak forecasts could be disseminated.

Beneficiaries of improved forecasts would include the National Plant Protection Departments (NPPDs) of sahelian countries affected by *O. senegalensis,* as well as the Lake Tchad Commission. As stated in the Project Memorandum, however, a further phase to provide a software package of the model is needed if NPPDs or international bodies express a wish to produce forecasts for themselves.

The follow up action/research necessary to promote the findings of the work to achieve their development benefit? (This should include a list of publications, plans for further dissemination, as appropriate).

The model has been validated using a relatively short time-sequence and, ideally, its output should be compared to *O. senegalensis* population data over a longer period to improve our confidence in the forecasts it generates. This may be possible if a funded collaboration can be set up between NRI, Cirad/PRIFAS and AGRHYMET. This linkage would then generate a natural route for promoting the findings of the work and achieving their developmental benefit.

A draft manuscript detailing the model, the methodologies used to generate the data sets and the results has been written and will be submitted to an appropriate peer-reviewed journal (see Output 4).

For projects aimed at developing a device, material or process specify:

a. *What further market studies need to be done?* Demand for improved forecasting tools clearly exists and was expressed by West African National Plant Protection Department (NPPD) staff at the International Conference on New Strategies in Locust Control, Bamako, April 1995. To confirm that this demand still exists, it would be useful for Drs Colvin and Holt to visit AGRHYMET, Niamey, to demonstrate the model to scientists there and to discuss ways of achieving the maximum developmental benefit from this work.

b. *How the outputs will be made available to intended users?* Dependent on the response to the activity proposed in (a), scientists at AGRHYMET could be trained in the use of the model and an electronic version handed over to them.

c. *What further stages will be needed to develop, test and establish manufacture of a product?* As mentioned above, the model has been validated using a relatively short time sequence and, ideally, its output should be compared to *O. senegalensis* population data over a longer period to improve our confidence in the forecasts it generates. The model in its research version is not in a form required for the standards of a modern software package. Substantial programming work would be required to create a product version for user-testing. Not only does the operation of the model need to be transparent and foolproof but also, forecast generation and CCD data entry need to be automated. A further cycle of programming would then be required to respond to problems raised and to deliver a software product.

d. *How and by whom, will the further stages be carried out and paid for?* As a first step, funding will be sought from the DFID CPP for a marketing study visit to AGRHYMET. One of the topics for discussion during this visit would be the identification of a funding source to pay for the inputs required to generate *O. senegalensis* outbreak forecasts. Funding will also be sought for a HEFCE PhD studentship, supervised jointly by NRI and PRIFAS/CIRAD staff.

Table 1. Egg-pod predation in October 1997 at field sites in northern Cameroon

Site	Total egg-pods	Intact egg-pods	*X. oophaga* present	*M. vicinalis* present	Unidentified predator
Kaele	24	14	1	0	9
Lara	8	3	0	0	5
Tchatibali	9	6	1	0	2
Maroua	3	1	0	0	2
Mokio	12	3	6	2	1
Mora	15	7	0	3	5
Wazan	18	3	0	0	15
Waza	11	0	0	4	7
Total	100	37	8	9	46

Table 2. Egg-pod predation in November 1997 at field sites in northern Cameroon

Site	Total egg-pods	Intact egg-pods	*X. oophaga* present	*M. vicinalis* present	Unidentified predator
Kaele	18	6	0	0	12
Lara	13	3	2	0	8
Tchatibali	21	5	0	0	16
Maroua	15	1	3	1	10
Mokio	27	7	0	3	17
Mora	10	2	1	1	6
Wazan	21	10	0	4	7
Waza	24	16	2	1	5
Total	149	50	8	10	81
Percent	100	33.56	5.37	6.71	54.36

Table 3. Parameter values for different season types. Rains start early or late, are wetter or dryer than average and retreat early, late, or stagnate in north/middle. Population change is scored in the range -3 to +4 (large decrease, moderate decrease, small decrease, no change, small increase, moderate increase, large increase, very large increase, respectively) and migration in the range 0 to 3 (none, few, moderate, most, respectively)

	Season type											
Start	Early						Late					
Quantity	Dry			Wet			Dry			Wet		
Retreat	E	L	S	E	L	S	E	L	S	E	L	S
Type No.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
Parameters												
r_1 S1 stay	0	0	0	1	1	1	0	0	0	1	1	1
r_2 S1 go	1	1	1	3	3	3	1	1	1	3	3	3
r_3 M eggs	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
r_4 N eggs	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
r_5 S2 stuck	0	0	0	1	1	1	0	0	0	1	1	1
r_6 M2 stay	1	1	1	1	1	1	1	1	1	1	1	1
r_7 M2 go	0	1	1	3	3	3	-3	1	1	3	3	3
r_8 N eggs	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
r_9 S3 stuck	-1	0	0	1	1	1	-1	0	0	1	1	1
r_{10} M3 go	1	2	2	1	3	3	1	2	2	1	2	2
r_{11} N3 go to S	1	2	2	2	4	4	-3	1	1	2	3	3
r_{12} M3 stay	-1	2	2	1	3	3	-2	1	1	1	2	2
r_{13} N3 go to M	-2	2	2	2	4	4	-3	1	1	2	3	3
r_{14} N3 stay	-2	1	1	2	4	4	-3	1	1	2	3	3
a_1 S1 go	3	3	3	3	3	3	3	3	3	3	3	3
a_2 M2 go	2	3	3	3	3	3	2	3	3	3	3	3
a_3 M3 go	1	3	0	2	3	0	1	3	0	1	3	0
a_4 N3 go to S	1	3	0	2	3	0	0	3	0	1	3	0
a_5 N3 go to M	1	1	0	1	1	0	0	1	0	1	1	0
v_1 Predators S	-1	0	0	2	2	2	-1	0	0	1	2	2
v_2 Predators M	-1	0	0	3	3	3	-2	-1	-1	2	3	3
v_3 Predators N	-2	-1	-1	3	3	3	-3	-2	-2	2	3	3

Appendix 1. Reasoning and assumptions relating to the effect of season types on *O. senegalensis* ecology and movement.

1. *Early start, dry, early retreat*. The rain reaches the northern zone but is patchy. The rains retreat from the northern and middle zones before adult emergence is complete, so the final O. senegalensis generation is incomplete at the end of the season.

2. *Early start, dry, late retreat*. The rain is patchy in the northern zone but there is sufficient time for the O. senegalensis population to complete the final generation of the season.

3. *Early start, dry, stagnation*. The population change is similar to (2), but stagnation causes adults of the final generation to be trapped in the middle and northern zones rather than migrate to the southern zone.

4. *Early start, wet, early retreat*. The rains reach the northern zone but retreat from the northern and middle zones before adult emergence is complete, thus the final O. senegalensis generation is incomplete. The season is wet so population increase is greater than (1).

5. *Early start, wet, late retreat*. It is very wet in the southern zone with some swamping and mortality by flooding. Food quality is initially very high but declines during the season in the middle and southern zones. A long, wet season allows a large number of generations to be completed.

6. *Early start, wet, stagnation*. O. senegalensis population growth is similar to (5) but stagnation means grasshoppers are trapped in the middle and northern zones at the end of the season.

7. *Late start, dry, early retreat*. There is insufficient rain for complete hatching. Vegetation quality is poor. Little rain reaches the northern zone. The rains retreat from the middle zone before adult emergence is complete.

8. *Late start, dry, late retreat*. As (7) but the season is sufficiently long for the final generation to be completed and migration to the southern zone to occur.

9. *Late start, dry, stagnation*. O. senegalensis population growth as (8) and movement as (6).

10. *Late start, wet, early retreat*. Hatching is complete and the rains reach the northern zone but retreat before adult emergence is complete.

11. *Late start, wet, late retreat*. Movement as (5), and population growth similar to (5), except with a shorter season there are fewer generations, so population growth in period 3 lower than that in (5).

12. *Late start, wet, stagnation*. Population growth as (11) and movement as (6).

Appendix 2. Summary of the rules governing parameter values as set out in Table 4.

Population change:

If the season is dry, r_1 & r_5 both equal 'no change', but if wet, then 'small increase'.

If the season is dry, r_2 and r_7 both equal 'small increase', but if wet then 'large increase'. There are exceptions when the season is dry: if the rains both start and retreat early when r_7 equals 'no change'; if the rains start late and retreat early the r_7 equals 'large decrease'.

r_6 equals 'small increase' irrespective of season type.

r_3, r_4 & r_8 equal 'small decrease' irrespective of season type.

If the season is wet, r_9 equals 'small increase', but if dry, 'no change', except if the season is both dry and the rains retreat early, then 'small decrease'.

If the rains retreat early, r_{10} equals 'small increase', otherwise 'moderate increase', except if the season is wet and the rains start early, then 'large increase'.

r_{11} equals 'large decrease' if the season starts late, finishes early, and is dry; otherwise an increase occurs: 'small', if the season is dry and starts and finishes early or starts and finishes late/stagnates; 'moderate', if the season is dry but starts early and finishes late/stagnates, or is wet but starts late and finishes early; 'large', if the season is wet and starts and finishes late/stagnates; and finally 'very large', if the season is wet, starts early and finishes late/stagnates.

r_{12} equals a decrease if the season is dry and finishes early, 'moderate' if the rains also start late, 'slight' if they start early; otherwise an increase occurs: 'small', if the season is wet and the rains retreat early, or if the season is dry and the rains start and finish late/stagnate; 'moderate', if it is dry and the rains start early and finish late/stagnate, or if it is wet and the rains start late and finish late/stagnate; and finally 'large' if the season is wet, starts early and finishes late/stagnates.

r_{13} is the same as r_{11} with the exception of a dry season which starts and finishes early when r_{13} equals 'moderate decrease'.

r_{14} is also the same as r_{11} with the exception of dry seasons which start early: r_{14} equals 'small increase' if the rains retreat late or stagnate, but 'moderate decrease' if the rains retreat early.

Migration

a_1 is equal to ‘most’ irrespective of season type.

a_2 is equal to ‘most’ except if the season is dry and the rains retreat early, then ‘moderate’.

a_3 is equal to ‘none’ if stagnation occurs, ‘most’ if the rains retreat late and ‘few’ if the rains retreat early. An exception is a wet season with the rains starting and retreating early when a_3 is ‘moderate’.

a_4 is equal to ‘none’ if stagnation occurs and ‘most’ if the rains retreat late; if the rains retreat early, then a_4 is ‘none’ if it is dry and the rains start late, ‘few’ if it is wet and the rains start late or dry and the rains start early, and ‘moderate’ if it is wet and the rains start early.

a_5 is equal to ‘none’ if stagnation occurs and ‘few’ otherwise. An exception is a late starting, early finishing, dry season when a_5 is none.

Change in mortality due to predators

If the season is wet then v_1 is ‘moderate increase’ except if the rains start late & retreat early, then ‘small increase’; if the season is dry then ‘no change’ except if the rains retreat early, then ‘small decrease’.

If the season is wet then v_2 is ‘large increase’ except if the rains start late & retreat early, then ‘moderate increase’; if the season is dry but the rains start early then ‘no change’ except if the rains retreat early then ‘small decrease’; if the season is dry and the rains start late then ‘small decrease’ except if the rains also retreat early, then ‘moderate decrease’.

If the season is wet then v_3 is ‘large increase’ except if the rains start late & retreat early, then ‘moderate increase’; if the season is dry but the rains start early then ‘small decrease’ except if the rains retreat early then ‘moderate decrease’; if the season is dry and the rains start late then ‘moderate decrease’ except if the rains also retreat early, then ‘large decrease’.