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An Ecological Model for the Study of the Grasshopper Oedaleus senegalensis in West Africa [and Discussion]

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An ecological model for the study of the grasshopper *Oedaleus senegalensis* in west Africa

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(*Paper presented* in absentia; *read by N. D. Jago*, *C.O.P.R.*, *London*)

This study concerns the Senegalese Grasshopper, *Oedaleus senegalensis*, which is one of the most damaging acridids to crops in the Sahel. The method used is an attempt to provide a satisfactory description of reality by ecological modelling. Functional analysis of interactions between the grasshopper and its environment has provided a scheme of relations which is the basis of the specific ecological model. Its credibility being established, the model is utilized where there is any shortage of information; it is also possible to include spot checks of the validity of the results by verifying that the known facts fit into the scheme obtained by deductive reasoning. Operational simulation has directed attention to: the essential elements in the life cycle of the species (seasonal displacements, range of distribution, development of generations); to the factors involved in mass multiplication and in gregarization in west Africa; and to the organization of an effective and economic system of surveillance and control.

1. Introduction

Oedaleus senegalensis (Krauss 1877) is a Sahel grasshopper which can cause heavy damage to cereal crops when numerous. So far it has been studied at various times and places by several workers, including Chopard (1950), Joyce (1952), Saraiva (1962), Bathia & Ahluwalia (1966), Batten (1969), Castel (1975) and Popov (1975). Their findings have provided a better understanding of this grasshopper, but have still been incomplete. In the course of the French programme of interdisciplinary research on Sahel grasshoppers (PRIFAS), in Upper Volta and Niger during 1975–6 (undertaken by GERDAT with the cooperation of the Aid and Cooperation Fund of the Government of France), further complementary studies have been undertaken. The extent of the observations available – new and old, personal and from the literature – appeared sufficient for attempting to construct an ecological model presenting the dynamics of natural populations.

2. Description of the ecological model

The initial hypothesis, in agreement with Holling (1964), is that much of the apparent complexity of the dynamics of the natural populations of *Oedaleus senegalensis* involves only a small number of ecological key factors. Study of the species in its natural environment suggests six such factors. These are: the photoperiod, the thermal, moisture and vegetation factors, the availability of the grasshopper, and the accessibility of the biotope. Combining the first four would suffice to characterize, on the macro- and meso-scale, the environment of the insect, and

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the last two its capacity to respond according to whether or not it is present on the biotopes concerned.

The range of conditions for survival is determined by a particular set of combinations of the six key factors. Within these limits a much narrower range defines the ecological optimum, where the grasshopper can best express its biological potential for speed of development and rate of survival. The factors of soil type and of natural enemies are not included here, since it has not been possible to obtain reliable data on a sufficiently extensive scale. These are more or less dependent on the other ecological factors which are included, and often reinforce their effects. The choice of key factors can be judged only by considering the implications of the model.

Table 1. Representative combinations of environmental factors to which the successive stages of *O. senegalensis* are subjected

(For legend see text, § 2.)

	factors				indices: eggs			indices: larvae			indices: adults				
number	F_3	F_4	F_5	F_6	V	S	R	V	S	R	V	S	R	A	D
1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
2	0	0	0.01	0	0	3	0	0	0	0	0	0	0	0	0
3	0	0	0.10	1	0	2	0	0	1	0	0	1	0	0	0
4	0	1	0	0	0	3	0	0	0	0	0	0	0	0	1
5	0	1	0.01	0	0	3	0	0	1	0	0	1	0	0	1
6	0	1	0.10	1	1	3	3	1	1	1	1	1	1	1	0
7	0	2	0	0	1	3	3	1	1	1	1	1	1	0	2
8	0	2	0.01	1	1	3	3	1	1	1	1	1	1	0	2
9	0	2	0.10	2	2	4	8	2	2	4	2	2	4	2	0
10	0	2	0.20	2	3	4	12	2	2	4	2	2	4	2	0
11	0	2	0.50	3	3	1	3	2	1	2	2	1	2	0	3
12	0	2	1.00	3	3	0	0	2	1	2	2	1	2	0	3
13	0	3	0	0	4	2	8	3	0	0	3	0	0	0	5
14	0	3	0.01	1	4	3	12	4	1	4	4	1	4	0	5
15	0	3	0.10	3	5	4	20	5	4	20	5	4	20	5	0
16	0	3	0.20	4	5	4	20	5	4	20	5	4	20	5	0
17	0	3	0.50	4	5	1	5	5	2	10	5	1	5	0	3
18	0	3	1.00	5	4	0	0	5	1	5	5	0	0	0	5
19	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	1	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
21	1	0	0.10	1	0	0	0	0	1	0	0	1	0	0	0
22	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
23	1	1	0.01	0	0	0	0	0	1	0	0	1	0	0	1
24	1	1	0.10	1	0	0	0	1	1	1	1	1	1	1	0
25	1	2	0	0	0/1	3	3	1	1	1	1	1	1	0	2
26	1	2	0.01	1	0/1	3	3	1	1	1	1	1	1	0	2
27	1	2	0.10	2	0/2	4	8	2	2	4	2	2	4	2	0
28	1	2	0.20	2	0/3	4	12	2	2	4	2	2	4	2	0
29	1	2	0.50	3	0/3	1	3	2	1	2	2	1	2	0	3
30	1	2	1.00	3	0/3	0	0	2	1	2	2	1	2	0	3
31	1	3	0	0	0/4	2	8	3	0	0	3	0	0	0	5
32	1	3	0.01	1	0/4	3	12	4	1	4	4	1	4	0	5
33	1	3	0.10	2	0/5	4	20	5	4	20	5	4	20	5	0
34	1	3	0.20	3	0/5	4	20	5	4	20	5	4	20	5	0

For lines 25–34 there are two different possibilities according to the time of year:

January–March: eggs developing, together with nymphs, at the varying rates shown.

October–December: eggs in diapause and development averted; indicated rate of nymph development to be disregarded, and $V = 0$.

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Supposing that the biotope is both available and accessible, then subsequent population growth is regulated by the four factors: photoperiod (F_3), thermal (F_4), moisture (F_5) and vegetation (F_6). In nature only a certain number of the possible combinations of these factors have ecological significance. For the model as envisaged, 34 situation-types have been used to represent the majority of the combinations of weather and environment that the insect is likely to encounter.

Representative types of environment are derived by considering:

Two classes of photoperiod: day length more than 12 h ($F_3 = 0$) or less than 12 h ($F_3 = 1$). The critical threshold for inducing embryonic diapause is of the order of 12 h for the females during their period of reproduction.

Four classes of mean shade temperature (measured in a meteorological screen):
less than 22.5 °C: development impossible, $F_4 = 0$;
22.5–25 °C: slow development, $F_4 = 1$;
25°–27.5 °C: rapid development, $F_4 = 2$;
more than 27.5°: optimum temperature, $F_4 = 3$.

Five classes of environmental humidity, measured by the ratio k between actual and potential evaporation. Its significance for the insect is deduced from field observations:
k = 0.00: environment totally dry, highly unfavourable;
0.01: environment dry, unfavourable;
0.10–0.20: optimum humidity;
0.50: environment too moist for the adults;
1.00: environment too moist for eggs, nymphs and adults.

Six classes of state of vegetation, described broadly by turgescence or by the proportion still green, expressed as an index varying from 0 (vegetation totally dry) to 5 (vegetation completely green), and depending largely on the other factors previously considered.

Having selected these 34 situations, we have then ranked and tabulated the responses of *Oedaleus senegalensis* in terms of several indices:

Development period index (V) ranging from 0 to 5. 0 is the slowest rate which can be observed for a given biological stage (egg, nymph, adult), and 5 the fastest. For eggs this is the duration of incubation, for nymphs the total period of development from hatching to final moult, and for adults the length of time from hardening of the cuticle, and including the complete maturation of the eggs in the females. (See table 2.)

Survival index (S) ranging from 0 to 5. 0 represents complete mortality, and 5 the best that could be observed in nature.

Combining these two indices gives an *index of success* (R) for each developmental stage:

$$R\,(\text{success}) = V\,(\text{speed}) \times S\,(\text{survival}).$$

In theory this index (R) ranges from 0 to 25. In reality it does not exceed 20, owing to mortality attributable to non-climatic factors which have so far been disregarded.

Indices of displacement of adults. These describe the probability of observing arrival (A) or departure (D) of adult populations. In both cases the index ranges similarly from 0 to 5, 0 indicating absence of displacement and 5 maximum flight activity; populations are carried in or out according to whether or not the environment is favourable to the adults becoming sedentary.

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The criterion of egg production is included implicitly in the indices of survival and of displacement of adults, for Launois-Luong (1979) has shown that in this species total egg production depends more on the number of females laying than on the number of eggs per pod or number of egg-pods per female.

In constructing table 1, showing the representative combinations of types of environment and the stages of the insect, the unit of time used is the decade (10 days). The inferences set out there have been based on three sources of data:

(i) field observations made in 1975 and 1976 under PRIFAS in different types of environment (the most frequent source);

(ii) earlier documents (a few cases); and

(iii) interpolation or extrapolation for those types of environment for which no entomological data were available. In these cases, which are rare, an estimate of the combined action of the separate key factors whose individual effect is known has been made (Launois 1978).

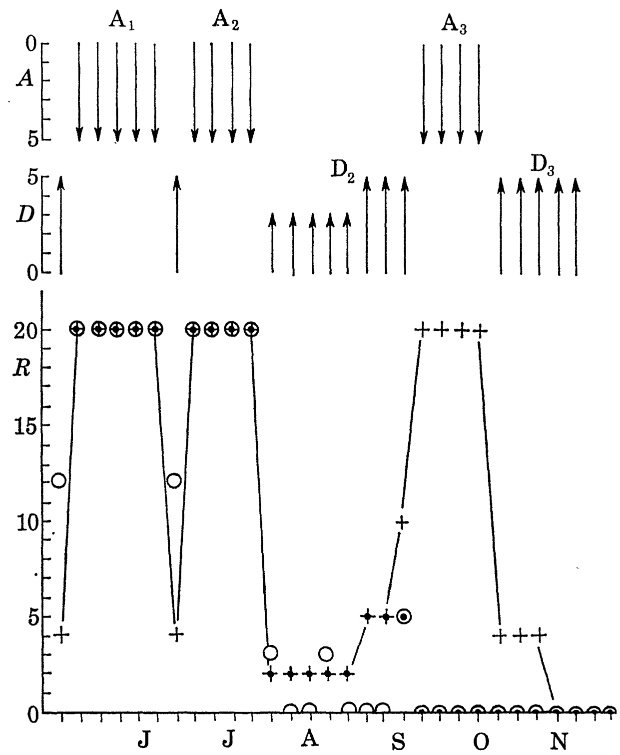

FIGURE 1. First stage of graphical presentation of the ecological model: variation with time of indices of success for eggs, nymphs and imagos, and of indices of arrival A and departure D of adult populations. +, R_a; ●, R_n; ○, R_e.

In considering mortality it is hardly possible to go beyond the indices 0–5. On the other hand, it has been possible to construct a second, more detailed table (table 2) to show the relation between the index of speed of development given in table 1 and the *real* duration of development for each biological stage in days; the latter is established from personal observations and is in agreement with the published data available.

This ecological model, specific to *Oedaleus senegalensis*, consists of use of a graphical presentation expressing the relations between parameters in a given environment, simply characterized, and the most likely responses of the species according to the developmental stages present.

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3. Method of use of the model

(*a*) *Graphical construction: first stage*

The indices of success for eggs (R_e), nymphs (R_n) and adults (R_a) are plotted as a function of time, by week or by decade, as in the example shown in figure 1.

The values obtained for each stage are joined by a line, following the indications provided by table 1. This graphic presentation is completed by plotting the indices of arrival and of departure of the adults, and also the limits of development (eggs entering diapause at the beginning of the dry season). In this way the periods favourable or unfavourable to each biological stage of the species are presented visually. Experience shows that the curve of the indices of success for adults often gives an idea of the index of actual abundance of the adult populations.

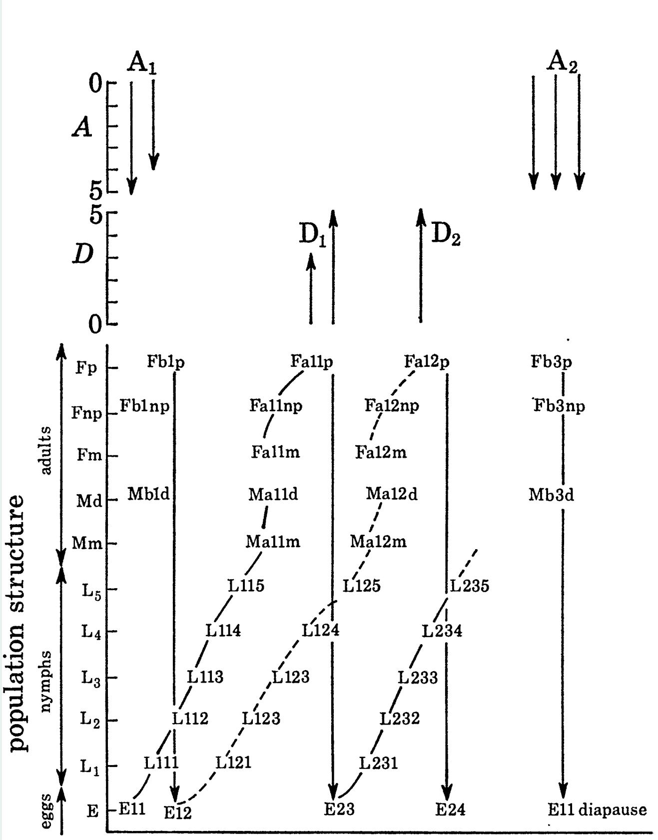

Figure 2

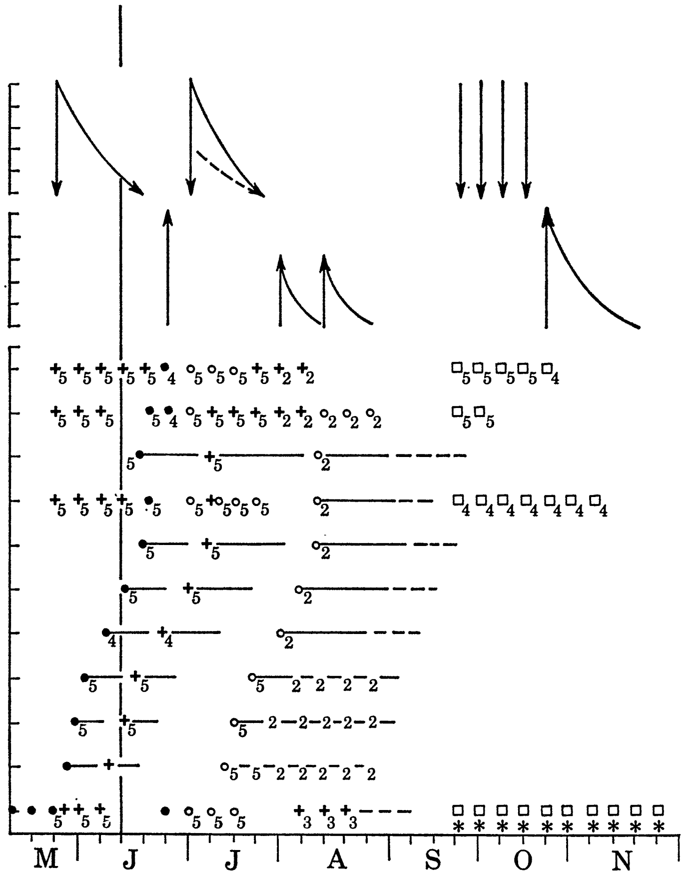

Figure 3

Figure 2. Second stage of the graphical presentation of the ecological model: timetable of life histories. The system used to describe the structure of populations is letters followed by 3 digits:

the first letter indicates the developmental stage, or for adults, the sex, the first digit denotes the rank of breeding, the second digit denotes the rank of the cohort, the third digit denotes the larval instar. For adults, the letter following the one indicating the sex indicates the origin of the insects, either locally produced (a) or immigrant (b). The final letter signifies whether the cuticles are still soft (m) or hardened (d), and whether the females have laid (p) or not (np). Eggs in diapause are shown with an asterisk.

Two examples of reading the code:

L123, nymph of the first rank of breeding, second cohort, third instar.

Fa12np, adult female locally produced of the first rank of breeding, second cohort, not yet laid eggs.

Figure 3. Theoretical reconstruction of the population at Maradi (Niger) in May–November 1975, to show an example of the procedure shown in figure 2.

(*b*) *Graphical construction: second stage*

The development of the structure of the population is now plotted against time, as in figures 2 and 3, which show eggs (E), nymphs (L_1–L_5) and adults: males with soft cuticles (Mm), with hardened cuticles (Md); females with soft cuticles (Fm), with hardened cuticles but not yet laid (i.e. nulliparous females) (Fnp), and those having already laid (i.e. parous females) (Fp). Above are indicated the indices of arrival (A) and departure (D) of adults, as in figure 1.

Table 2. Definition of developmental period index (V) in terms of actual duration times of each developmental stage

(Diapause of 5–9 months.)

		nymph instars: period (days)					adults	
V	eggs: duration of incubation	1	2	3	4	5	hardening of cuticle days	interval before just laying days
5	15	4	3	5	5	5	3	10
4	20	6	6	8	9	9	5	15
3	30	10	10	14	17	17	9	25
2	50	18	18	26	33	33	17	45
1	90	34	34	50	65	65	33	85
0†	—	—	—	—	—	—	—	—

† $V = 0$ corresponds to no growth.

Generally the study begins at the first rain marking the end of the dry season. The eggs have therefore completed their diapause and are ready to continue their development as soon as the water balance in the soil becomes favourable. A first cohort of nymphs is identified whose development can be followed regularly by applying tables 1 and 2, decade by decade. When the fledglings appear, their development on site or their departure is inferred by the same procedure. When environmental factors permit laying in the same locality, a second generation occurs and its development can be traced in the same way.

At the same time as the hatching observed to follow the first effective rains, the biotope where it occurs is usually colonized by immigrant adults produced in areas which had received rain earlier. The immigrant breeding females can lay on the site and give rise to descendants (second cohort of nymphs) whose development can be followed similarly.

At the end of the wet season, the females experienced a photoperiod of decreasing day length and produce diapausing eggs. The eggs remain in diapause throughout the dry season. Finally, this treatment of the data can be completed by incorporating the relative importance of the populations available from different starting points, when this is known, and by examining the indices of success presented in table 1.

By analysing thus the development of local populations, reproduction by reproduction, cohort by cohort, the whole picture of population dynamics can be built up.

4. Validity tests on the model

Several types of validity tests have been carried out on the ecological model. The first tests relating to the area for which the model was initially developed, Maradi in Niger, simply verify its consistency with the local conditions.

Test 1 relates to the period 12 May–6 December 1975. The meteorological data were provided by ASECNA, the entomological data by our survey teams. The agreement between what actually happened and the deduced sequence of events was satisfactory for 14 basic events of the type: hatchings, identification of individual cohorts of hoppers, dates of fledging, major arrivals and departures of adults, periods of laying. As the model had been devised from the observations made that same year in the same sites, this was simply a test of the consistency of the model.

Test 2 was concerned with the period 10 May–5 December 1976. As previously, the data on the environment and on the grasshoppers had been obtained separately, and the deductions on the development of the populations were based solely on the environmental data. Of 16 basic events indicated by the application of the model, four could not be verified by reference to the actual population events, and concerned inferred arrivals of immigrants, and their progeny, which did not occur as predicted by the model because of the scarcity of immigrant adults. It may be deducted from this that the good results obtained from the first test had been due to the high level of insect numbers available throughout the rainy season of 1975. Because of this all the potential entomological events were realized. By contrast, in 1976 this favourable situation did not recur. This indicates that optimal use of the model requires factors F_1 (availability) and F_2 (accessibility – including consideration of wind-systems), of biotopes, obtained either by direct observation, or by application of the model to the entire distribution area of the species.

The next series of tests concerned natural situations in places and conditions remote from those on which the model had been devised, and permitted an assessment of its general applicability. The observations on both the environment and the grasshoppers had been made by Lecoq (1978) at Saria in Upper Volta and in the Sudano-Sahelian zone, not in the Sahel itself.

Test 3: for the period from August to December 1975, the three insect events deduced from the model were in effect observed in the field.

Test 4: the insect developments of March to December 1976 at Saria, inferred by running the model, were shown to be correct; all 8 events could be verified. In this test account was taken of whether insects were available at the beginning of the rainy season, and this improved the results.

These four tests against actual events show that the simplified picture presented by the model does indeed resemble the real situation, supporting the choice of parameters. The model may therefore help to compensate for lack of knowledge, experience and observation in seasonal displacements, the distribution area of the species, and the general features and special characteristics of each generation, if it may be assumed that the environment/grasshopper relations in these cases are comparable with those which have already been verified against actual field situations.

5. Characteristics of seasonal displacements

In view of the repeated coincidences on the one hand of adult grasshoppers being brought into an area and the onset of favourable conditions and, on the other hand, of the departure of adults with the environment becoming unfavourable (too dry, or too wet, for example), it is suggested from the model that *O. senegalensis* needs to cover 500–800 km during the hot season if it is to remain as long as possible in ecological conditions suitable for breeding, and the maintainance of the species (represented by a monthly rainfall of about 25 mm). Generally such directed displacements are facilitated by convergent windfields in zones where rainfall is most likely to be produced (Rainey 1951). The resultant seasonal displacements are generally southwest/northeast. The adults emigrating from south to north during April–July stop in August to the north of the Sahel and in the southern parts of mountain massifs such as Adrar in Mauritania, Adrar des Iforas and Aïr; their progeny return southwards with the movement of the intertropical front in September, October and November. Subject to knowing also the degree of abundance of adults during the hot season, variations between years can be interpreted in this way. The ability to fly long distances is certainly one of the most remarkable adaptations of this acridid to the unstable conditions of its environment in the hot season.

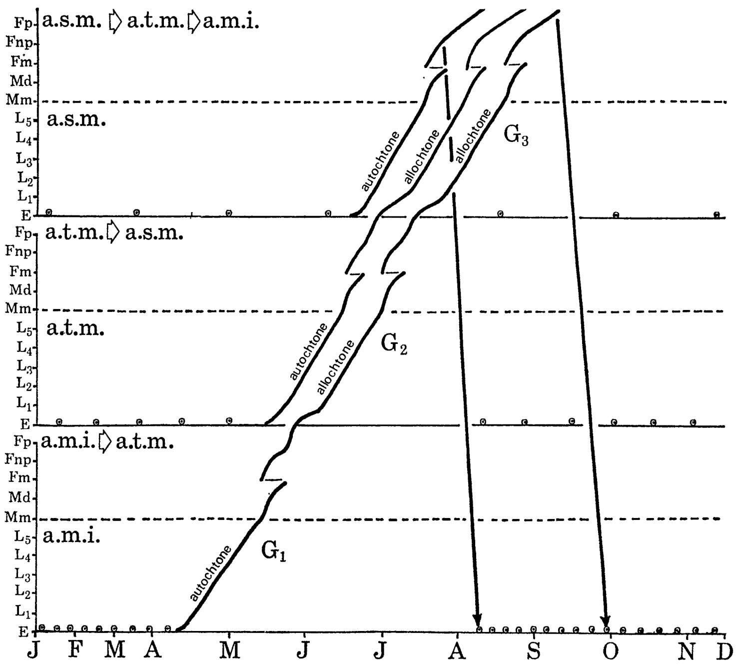

FIGURE 4. Schematic presentation of the biological cycle of *Oedaleus senegalensis*: three generations in the hot season and an egg diapause in the dry season, in the three habitats which make up its distribution zone in West Africa. For population structure see figure 2. For legend see text. Autochtone, locally produced; allochtone, immigrant. ⊙, eggs in diapause.

6. RANGE OF THE SPECIES

The northern and southern limits of the distribution area of *O. senegalensis* have been described by Batten (1969); the fact that they are also suggested by the model helps to validate the latter. Schematically, the northern limit coincides with the 25 mm isohyet for August, and the southern limit with the same isohyet for October.

Study of the development of populations throughout the area in terms of seasonal changes, moreover, enables three areas, ecologically complementary for the insect, to be recognized.

Area of initial multiplication (a.m.i.) in the south, where development begins at the start of the wet season. This area generally operates in April and May, then again in November. It is bordered by the annual isohyets of 750 and 1000 mm.

Transitional area of multiplication (a.t.m.) in the middle, between the annual isohyets of 500 and 750 mm; generally operative in June, July and October.

Northern area of multiplication (a.m.n.) in the north, between the 250 and 500 mn annual isohyets, generally operative in August and September.

Recognizing these areas and their year-to-year variations greatly facilitates the description of the biological cycle of the species.

7. Succession of generations

By deducing (figure 4) the development of the generations throughout a normal year in the three areas identified above, we may distinguish three generations, G_1, G_2 and G_3, during the hot season each year.

The G_1 eggs are in diapause through the dry season. The first generation, G_1, appears in the a.m.i. The G_1 adults then move to the a.t.m. and give rise to the second generation, G_2. The G_2 adults breed in the a.n.m. to produce the third generation, G_3. The G_3 adults displace in the opposite direction to their forebears and return via the a.t.m. to the a.m.i., there to lay the next G_1 eggs.

Thus these three successive generations are possible only because the adults move in response to the meteorological conditions. In view of this system, it is not surprising that it has long been thought that there were only one or two generations. There is only one in the a.m.n. and two in the a.t.m. or a.m.i. It is possible to find three partial generations in the two latter areas, but the G_2 is often very limited.

8. Origin of outbreaks

Whether local or widespread, outbreaks of *O. senegalensis* are explained by optimum ecological conditions persisting in the same area, or by conditions favourable to the insect's biological cycle developing and synchronizing directly with it in time and space. In the latter case, the population explosion results from the optimization of the basic system.

In zones of developing irrigation the grasshopper has a better chance than elsewhere to find conditions favourable for its multiplication, which makes these areas more vulnerable. The aptitude of *O. senegalensis* for gregarization is weak; the critical threshold density for gregarious behaviour is at least of the order of 50000 adults per hectare, and this situation is exceptional.

By using the model in the framework of the years 1971–74, an explanation can be offered for the outbreaks of 1974. They had both longterm and immediate causes. The longterm causes arose from the drought that the Sahel experienced in 1971, 1972 and 1973: a progressive concentration of insects developed in the a.m.i. as a result of the reduction in the seasonal range of population movement on its northern side. The outbreaks of 1974 resulted from laying at high density at the end of 1973 by the G_3 parent generation whose losses by dispersal had been minimal. Other factors were certainly present but were secondary (reduction of predators). The subsequent (G_2) and following (G_3) outbreaks appear to have been simply the continuation and occasionally a reinforcement of the first outbreaks (G_1), since the rains of 1974, while greater than in the previous years, were not exceptionally high.

9. Conclusion

The production of a table to show the relations on a 10 day time-scale between those types of environmental conditions most frequently encountered in West Africa, and the most likely responses of *Oedaleus senegalensis* at the different biological stages in which it can occur, is the

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basis of the specific ecological model proposed. The systematic application of this table permits analysis of the dynamics of the grasshopper populations, not only qualitatively, but also providing some quantitative appreciation of the relative importance of the different cohorts. Tests on field data and on data from the literature appear to validate the model which is therefore seen as a tool for ecological investigation which is of value in fields such as seasonal displacements, breeding areas, the succession of generations and the interpretation of the outbreaks of 1974, where information is lacking. Thus this descriptive model could become a forecasting model opening up new avenues in monitoring the grasshopper and locust pests of the Sahel.

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Discussion

D. Yeo (*formerly Director, International Migratory Locust Organization* (*OICMA*), *Mali*). How soon does the author think that his findings might reach the stage of being of use to the Director of a control organization?

M. Launois. If it is accepted that this model has been validated, as the forecasts made in 1976 and 1977 for Niger, and found correct, appear to show, one might perhaps imagine a survey system based on its systematic use. For that it would be sufficient to collect regularly data on the environment, with the help of a project such as AGRHYMET (UNDP/FAO, Centre for Agrometeorology and Applied Hydrometeorology), to feed them into the model and from them to deduce the most likely responses of *O. senegalensis* in each natural region considered. The validity of the inferences should be checked in the field at strategic sites, where indications of the availability of this species could also be noted. While taking the minimum of risks, it would not be necessary to survey an entire country to obtain an accurate idea of the grasshopper situation. Two mobile survey teams should suffice in the hot season for each country of the Sahel. It would also be desirable to strengthen the inter-state arrangements for the exchange of grasshopper information, since *O. senegalensis* crosses political frontiers every year (e.g. Nigeria and Niger).

The resulting improvements to be expected in control operations would be particularly in locating areas where outbreaks might form, and in the timing of control to obtain the most lasting effects.

At the present state of the ecological model, operation is manual; in other words it is necessary to process individually each step needed in analysing the dynamics of the populations. We hope shortly to reduce the time needed to process the data by using a computer, which seems possible since all the operations required are logical and objective. When this stage has been reached, three types of forecast could be provided with very little delay after obtaining the basic data:

(i) Short-term forecast, of the order of 10 days, either presenting all the possibilities the environment can produce and their effects on the insect, or restricted to determining what might happen in the most favourable or least favourable conditions possible, reality being somewhere between the two.

(ii) Medium-term forecast, of the order of a month, indicating what is possible or not possible according to the biological limits for the development of the species.

(iii) Long-term forecast, from the beginning of one dry season to the beginning of the following wet season, made possible because of the existence of embryonic diapause. This could only be a forecast of what could happen at the worst.

In all these cases, grasshopper forecasting is strictly dependent on meteorological forecasting.

Finally, if one of the countries of the Sahel were to express the intention to put into effect a survey network based on this principle, it would probably need two years for it to become operational, bearing in mind the time needed to train staff and to set up the system in the field.

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