Ecology and Population Dynamics of Solitary Red Locusts in Southern Madagascar

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Abstract

This paper summarizes eight years of field study on the Red Locust, *Nomadacris septemfasciata* (Serville) in southwestern Madagascar and presents management recommendations for its control. This crop pest exhibits a fairly uniform annual life-cycle phenology in southern Madagascar, which involves seasonal migration and adult reproductive diapause. There is one generation/y. Eggs are laid at the beginning of the rainy season in November and December. Eggs hatch in 24-36 d, and the hatchlings reach adulthood in 50-70 d. Fledgling adults enter a reproductive diapause in March and April, and then migrate north and northeast to higher elevations (refuge area where rainfall is > 80 cm/y) where they remain throughout the dry season (May-October). In November (the beginning of the rainy season), the adults migrate south and west to lower elevations (breeding area where rainfall averages 40-80 cm/y) where they mate and initiate oocyte development. Females possess ~ 162 ovarioles, and typically lay two or three egg pods, each containing ~ 100 eggs. The six-month adult reproductive diapause is controlled by photoperiod. Eggs and nymphs can experience high mortality, and hence, these stages are key to predicting population dynamics. Based on our findings, we recommend concentrating surveys in the main breeding areas (including one small southwestern fringe with the strongest probability of gregarisation and outbreak), better monitoring of local rainfall abundance and distribution, and better monitoring of deforestation, which increases locust habitat.

Résumé

Cet article est le résultat de huit années d'études de terrain sur le Criquet nomade, *Nomadacris septemfasciata* (Serville) dans le sud-ouest de Madagascar et propose des recommandations pour la gestion préventive de cette espèce. Ce ravageur présente un cycle biologique annuel relativement uniforme dans le sud de Madagascar. Il n'y a qu'une seule génération par an, des migrations saisonnières et une diapause imaginale. Les oeufs sont déposés au début de la saison des pluies, en novembre et décembre. Ils éclosent en 24-36 jours, et les jeunes larves atteignent le stade imaginal en 50-70 jours. Les jeunes imagos entrent en diapause reproductive en mars et avril, puis migrent vers le nord et le nord-est vers des zones d'altitude plus élevée (zone refuge recevant plus de 800 mm de pluie par an) où ils demeurent pendant toute la saison sèche (mai-octobre). En novembre (début de la saison des pluies), les imagos migrent vers le sud et l'ouest vers les zones plus basses (zone de reproduction recevant entre 400 et 800 mm de pluie par an) où ils s'accouplent et commencent leur maturation sexuelle (développement des ovocytes). Les femelles possèdent en moyenne 162 ovarioles et déposent deux ou trois oothèques, chacune contenant environ une centaine d'oeufs. Les six mois de diapause imaginale sont controlés par la photopériode. Les oeufs et les larves peuvent subir une forte mortalité et, en conséquence, ces étapes sont essentielles pour prévoir la dynamique des populations. Sur la base de nos travaux, nous recommandons de focaliser et de renforcer la surveillance dans la zone principale de reproduction (dont une petite frange sud-ouest présente la plus forte probabilité de grégarisation et de pullulation), de mieux suivre l'abondance et la distribution des pluies, et de porter une grande attention au déboisement susceptible de créer de nouveaux habitats favorables.

Key words

Introduction

The Red Locust, *Nomadacris septemfasciata* (Serville) (Orthoptera: Acrididae) (Fig. 1), is a major crop and pasture pest throughout central and southern Africa (FAO 1967, COPR 1982). This species undergoes phase transformation and its outbreak areas are mainly located in the Great Lakes region of East Africa, in Tanzania, Zambia, Malawi and Mozambique (Bahana 1999, Bahana & Byaruhanga 1999). The last important plague ran from 1930-1944, started from the Great Lakes region and extended to a large part of Africa south of the Equator (Morant 1947). This pest still threatens Africa, where regular outbreaks with gregarious swarms are frequently reported and controlled by the International Red Locust Control Organization for Central and Southern Africa (IRLCO-CSA) (Musuna 1988).

In Madagascar, the Red Locust is also a long-standing crop pest (Têtefort & Wintrebert 1967). The first gregarious swarms were reported in the 1930s by Frappa (1935, 1936, 1938) with the beginning of locust research on the island and the installation of the first locust center in Betioky; this was in the extreme-south, in the middle of the outbreak area of the Migratory Locust, *Locusta migratoria* Linné, the main pest locust in this country. The Red Locust is found throughout the island (Franc *et al.* 2007), but apart from frequent reports of hopper bands and local swarm activity, no large, long-distance invasions have been reported (Frappa 1947; Têtefort & Wintrebert 1963, 1967; Randrianasolo 1978; Scherer 1997). However, on Madagascar, this species has continued to be a major concern, due to the extent of the crop damage it inflicts more or less every year, and to its spectacular migratory flights.

During the last 15 y, the Red Locust has caused increasing economic damage in Madagascar. Large-scale Red Locust outbreaks recently occurred, in conjunction with the Migratory Locust plagues of 1996-2000. For the first time in recorded history, these outbreaks damaged crops throughout Madagascar from the south to the north. The well-known outbreak area in the extreme south — regularly monitored by the National Antilocust Centre (NAC) — continued to be affected. However, in the northern part of the island, a new outbreak area appeared from 2000 to 2003, probably influenced by increased human activities, primarily deforestation (Franc *et al.* 2008). These outbreaks stimulated new research on the Red Locust in Madagascar, resulting in a better understanding of its biology and ecology, the characteristics of the solitary and gregarious phases, and the gregarization thresholds both for hoppers and adults (Franc *et al.* 2005, 2007, 2008, 2009; Lecoq *et al.* 2006, 2011). These recent works also suggest that in the southern tip of Madagascar the Red

Locust migrates seasonally from north to south and back, in synchrony with annual rainfall and wind patterns (Lecoq *et al.* 2006). In this paper, we now detail this migration, based on nearly eight years of field observations in the south of Madagascar. We also document the population dynamics, and the underlying ecological conditions that influence population, migration, gregarization and outbreaks of the Red Locust in southern Madagascar. Based on this new knowledge, we propose new management strategies to control this pest.

Methods

General study area: elevation and vegetation.—Our studies were carried out in southwestern Madagascar (Fig. 9), in an area regularly monitored by scouts from the Malagasy National Antilocust Center (CNA 2011). This 60,000 km^2 area extends between the Mangoky and Mandrare rivers in the most arid part of Madagascar. The west and southern portions of the study area are coastal, and most of the eastern portion lies in the border of the central plateau of Madagascar, at elevations between 500 and 1000 m.

Much of the area has been deforested and the native vegetation replaced in several areas by grassy formations, croplands and more-or-less wooded wastelands (Moizo 1997, Milleville *et al.* 1999, Casse *et al.* 2004). In the northeast, the landscape is open, desolate with small, remnant stands of evergreen forest restricted to valleys and other protected sites, surrounded by vast expanses of monotonous secondary grassland (steppes and savannas). These areas are almost totally devoid of trees, and have been subjected to regular annual burning for centuries, resulting in an irreversibly impoverished landscape.

Different plant species dominate, according to the topography and the degree of erosion. *Heteropogon contortus* is the commonest grass on soils not subject to waterlogging. *Loudetia simplex* and *Aristida* spp. occupy degraded slopes, and *Hyparrhenia rufa*, *Hyperthelia dissoluta* and *Cynodon dactylon* occupy low-lying areas which may receive runoff. The steppe and savanna vegetation in the northeastern zones changes to wooded (xerophilic bush) in a fringe of about 100 km along the southwestern coast, where conditions are even drier. This bush is dominated by members of the endemic family Didiereaceae and by shrubby and arborescent species of *Euphorbia*, such as *E. stenoclada*. Introduced cactus, such as *Opuntia* spp., are characteristic fodder plants of the extreme south (Humbert 1955, Anonymous 2011).

Rice, corn, sorghum, cassava, and beans are the main food crops in the extreme south (Antandroy and Mahafaly areas), and are frequently grown around the villages in permanent fields enclosed by hedges. A system of shifting cultivation is frequently practiced in the arid, sparsely populated regions of the far south and southwest. The dry bush or grassland is burned off, and drought-resistant sorghum or corn is sown in the ashes. Cattle are common in south Madagascar, and almost every family owns some zebu cattle. The usual practice is to allow the animals to graze almost at will. Farm-

Fig. 1. The Red Locust: solitary hopper (6th instar) and adult. Photos: M.H. Luong-Skovmand (hopper) and M. Lecoq (adult).

ers typically burn off the dry grass to promote the growth of new vegetation for animal feed.

General study area: climate.—The southwestern portion of Madagascar has a rainy season November to April, followed by a dry season from May to October. Annual rainfall varies with altitude, with ~ 100 cm/y in the central highland foothills in the northeastern sector of the study area, but only ~ 30 cm/y along the coasts at the southern tip of the island. During the rainy monsoon season, winds blow from the northeast toward the southwest. During the dry season, winds blow from the south and southwest toward the north and northeast (Duvergé 1949, ORSTOM 1973). Temperature varies with season and elevation. At the southwest coast in Tuléar, the mean monthly temperatures [(Tmin + Tmax)/2] are around 28°C during the rainy season and 20°C in the dry season. In contrast, at Ihosy in the interior highlands at ~ 760 m, these values are 25°C and 17°C, respectively. Temperature correlates with daytime length, which is longest (13 h and 1 min) in December, and shortest (10 h and 38 min) in July. In sum, the two seasons differ strongly in precipitation and wind direction, and moderately in temperature and length of daytime. The primary climate difference between the coastal and highland regions of southwest Madagascar is not photoperiod or temperature, but rainfall.

Life-cycle of the Red Locust in southern Madagascar.—In Madagascar, as in Africa, the Red Locust produces just one generation a year. Mating and egg laying occur in November and December at the onset of the rainy season, which lasts until April. Female Red Locusts generally lay eggs two or three times, with a clutch of 20-100 eggs for gregarious locusts and 20-195 eggs for solitary locusts. The eggs hatch after 24-36 d of incubation. The hoppers begin appearing in December. The hopper development period (6 moults in the gregarious phase, 7 for the solitarious) lasts almost two months (range 50-70 d) and the new-generation adults appear in March-April. The young adults harden their cuticle in ~ 10 d. They then enter reproductive diapause to survive through the dry season (May-October). Both sexual maturation (mating) and reproductive maturation (oogenesis in the ovaries) coincides with the first rains (Frappa 1935; Têtefort & Wintrebert 1963, 1967; Descamps & Wintrebert 1966; Randrianasolo 1978; Randriamanantsoa 1998). Hind wing color darkens with age (Norris 1959). Initially hyaline in the young adult, wings pass from pink (around March) to red-rosy (in June) and to purple-red (in July). This change of color is not related to sexual maturity, as recently asserted by Franc & Luong-Skovmand (2009), since sexual maturation starts only around November after the wings have already darkened.

Field surveys of locust populations and ecological conditions.—Field observations and samplings were conducted twice a week, between 2001 and 2008, at two sites located in the main outbreak area of the Red Locust. The first, near the village of Beomby (lat 24°13′04″S, long 44°15′58″E, elevation ~ 350 m) (Fig. 9), on the Mahafaly plateau, not far from the small city of Edjeda, was followed from May 2001 to Dec 2003. The second, near Ankiliarivo village (lat 23°47′06″S, long 44°23′16″E, elevation ~ 300 m) (Fig. 9), at the foot of the Mahafaly plateau and close to Betioky city (primary home of the National Antilocust Center), was surveyed from Dec 2005 to May 2008. In total, 521 surveys were carried out (280 in Beomby and 241 in Ankiliarivo).

Sampling was conducted in the typical habitats of the Red Locust (*i.e.*, shrubby high savannahs with hydromorphic black clay soil, covered with tall grasses). During each sampling, we attempted to collect the following data: **hopper density** (calculated as the mean

of 50 visual estimates, each taken from a different 1-m² surface), **adult density** (calculated as the mean of 10 visual estimates, each within a different 1 × 100-m area), and **population age structure** (divided into 7 different instars, soft adults, premature females, seven categories of mature females and old females). We recorded the reproductive state of adult females as follows: **premature** females (primary oocytes small and not yet developed, white or translucent, with no yellow yolk), **mature females before first laying** (yellow yolk deposit in primary oocytes; four classes according to the length of the primary oocytes (= the first row of oocytes): <1/4, 1/4-1/2, 1/2-3/4, >3/4 of the maximal 6-mm length), **postoviposition females** (1st, 2nd or 3rd egg pod already laid, based on the number of white follicle resorption bodies at the base of each ovariole — Albrecht 1956, Launois-Luong 1978, Sundberg *et al.* 2001). In **old females**, the integument is dull and dark-colored, with numerous pigmented maculae, and the insect is often damaged, particularly the wings (Lecoq & Mestre 1988). In total, we collected 7,421 hoppers and dissected 3,028 adult females, from the two sampling sites. For the 2001-2002 season, we estimated the **number of eggs deposited in the field**, at each laying, based on dissections of ovaries and counts of the number of follicle resorption bodies. As in other grasshoppers, one follicle resorption body is deposited at the base of the ovariole for each egg laid (Lecoq 1975, Launois-Luong 1978, Sundberg *et al.* 2001). We recorded **phase status** (solitarious, transiens, gregarious) for both nymphs and adults, based on integument color (Michelmore & Allan 1934, Faure 1935, Lecoq *et al.* 2011). We also collected **environmental data**, including: daily rainfall, air temperature and humidity (on an hourly basis, using a MicroLog 8-bit EC650 from CIMA TECHNOLOGIE, France) and height and greenness of grass by visual estimate at each survey.

Rainfall at these two sites (Ankiliarivo and Beomby) averages between 50 - 60 cm/y. Most of the rains fall between November and April. Dry periods, sometimes of more than one month, can be intercalated in the course of the rainy season. The height of the herbaceous vegetation is maximum near the end of the rainy season, between February and April. The vegetation greenness reaches 100% from the beginning of January to mid-March. The mean monthly temperatures at this altitude vary between 13 - 25°C (min. - max.) in the heart of the dry season (June, July, August) and 25 - 42°C (min. - max.) at the beginning of the rainy season (November-December). The mean maximum monthly temperatures drop notably in the middle of the rainy season (January to March) to be around 37°C. During the rainy season, the mean monthly relative humidity normally ranges between 50-90% RH (min. - max.), and during the dry season, it normally ranges between 15-70% RH (min. - max.). Bush fires are very frequent in the dry season, from April to October when one observes from 1 to 4 bush fires per month (1.5 on average) on our two sampling sites.

Scouts from the National Antilocust Center normally survey the entire southern part of the Island throughout the year, to check the population level of the Red Locust. Between 2001 and 2007, 7368 surveys were carried out. Some sites were surveyed more regularly and more intensely: some were surveyed once or twice per decade, but more generally between 12 and 22 times during the year, and mainly between October and May. The years 2004-2005 and 2005-2006 were selected for analysis because surveys were more abundant (respectively 1,461 and 1,416) and more regularly distributed in time (72 sites on the whole, including 60 analyzed for the season 2004-2005 and 58 for the season 2005-2006, the sites not being all the same from one year to another). On these 72 sites, we analyzed hopper and adult densities, and the age structure of the hopper population. We also recorded monthly rainfall throughout the study period (2001-2008) across all of south Madagascar from a
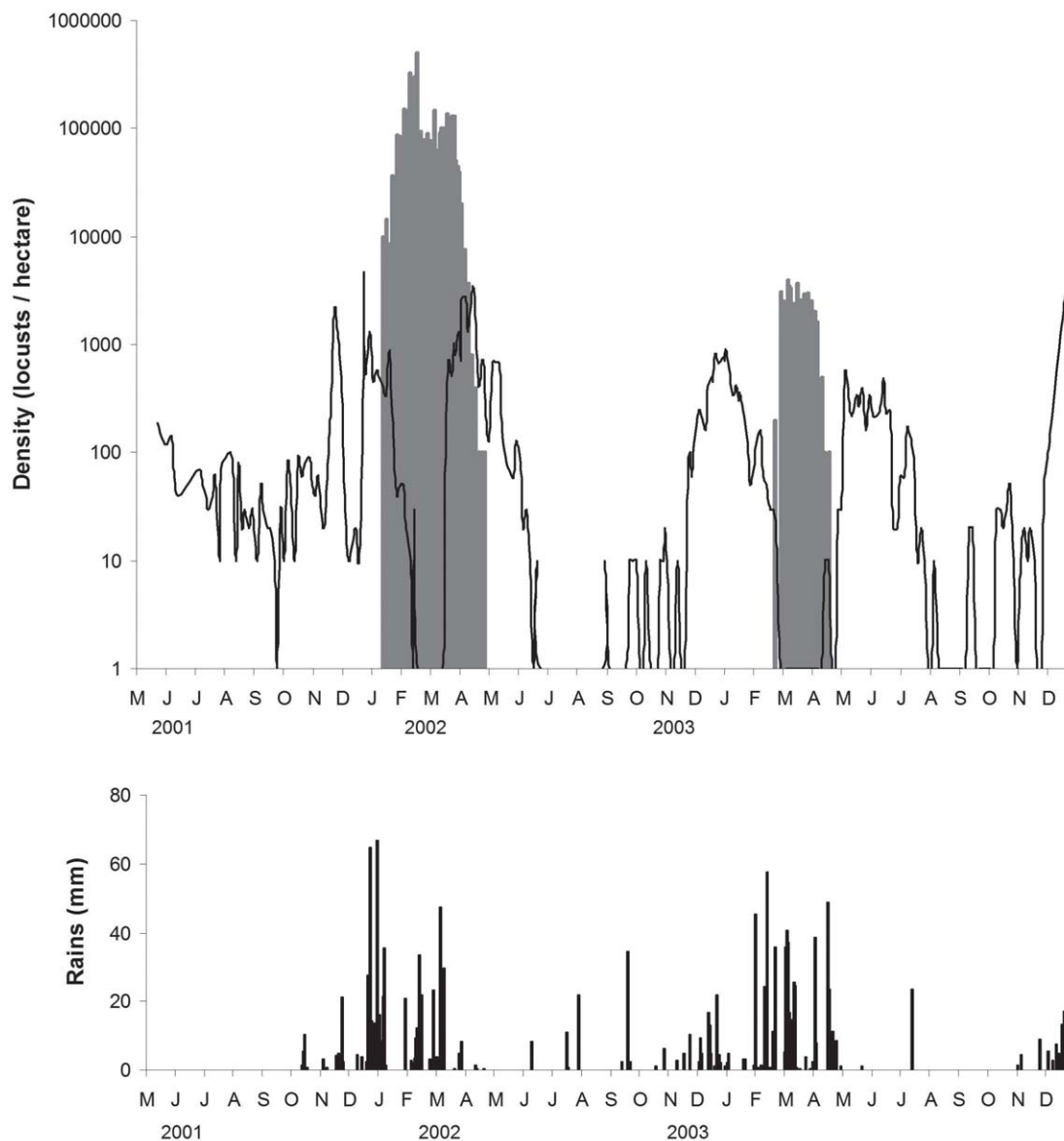
Fig. 2. Rainfall and densities of the Red Locust from May 2001 to December 2003 at Beomby (hoppers = grey area; adults = black line; rains = histogram). Density scale logarithmic. Monthly tic mark indicates month onset.

network of 115 rainfall stations belonging to various organizations (Malagasy National Antilocust Centre, Famine Early Warning System, HASYMA cotton company, Malagasy Central Meteorological Office, etc.). The precipitation for the sites not having rainfall stations was determined by interpolation using the rainfall maps.

During our 8-y study, monitored locust populations were mostly of low density, often less than 1,000 adults/ha or 50,000 hoppers/ha, thus much lower than the phase-transformation threshold, which is estimated to be around 5,000 adults/ha (Spurgin & Chomba 1999, Franc *et al.* 2005) or 100,000 hoppers/ha (Lecoq *et al.* 2011). For the two years (2004-2005 and 2005-2006) studied more intensely (2,877 surveys throughout south Madagascar), we observed only eight cases with adult densities higher than 5,000/ha (max. 30,000) and 35 cases with hopper densities higher than 100,000/ha (max. 1,000/m²). Red Locusts could thus be considered during all this period to be mostly in their solitary phase, apart from a few exceptional situations corresponding to very localized outbreaks. In Ankiliarivo and Beomby, the maximum adult densities were respectively 2,270/

ha and 4,600/ha and that of hoppers 51,400/ha and 498,000/ha (with only 12 cases where the density of hoppers was higher than the gregarization threshold).

Data analysis.—Beomby and Ankiliarivo data were analyzed in order to elucidate the life-history, migration cycles and reproduction rate of the Red Locust, and the impact of ecological conditions on these features.

For the 72 sites supervised more intensively by NAC in 2004-2005 and 2005-2006, for each locality, the annual population dynamics of the Red locust was established by examining density variations for the different hopper and adult instars (hopper instars 1 to 7, fledgling locusts, immature females, mature nulliparous females and females that had already laid eggs). This allowed us to determine different seasonal patterns among different sites and zones, and deduce the general life-history and adult migration patterns.

Then a few simple indices were calculated to characterize breeding patterns at each of these 72 localities for each year, including:
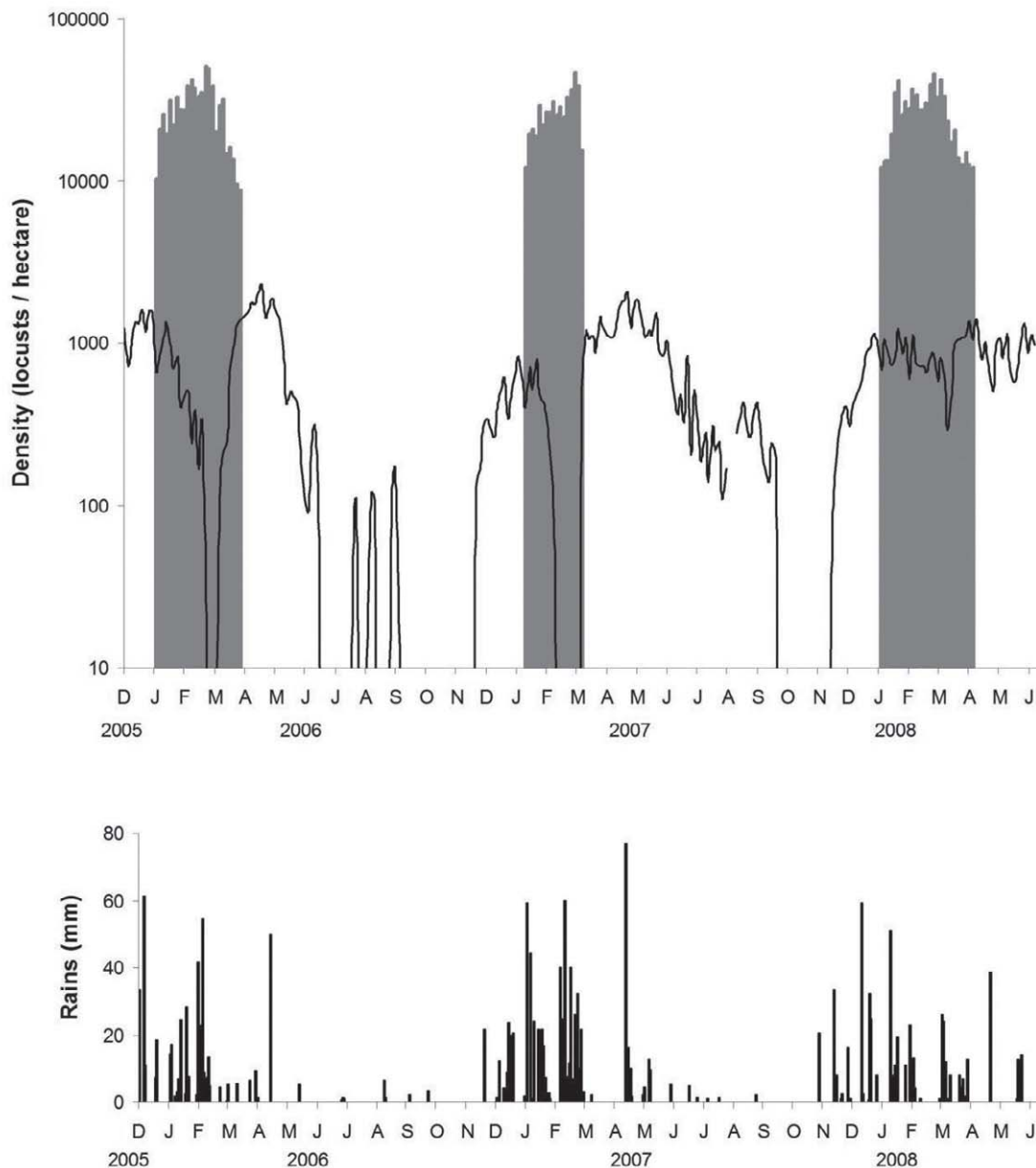
Fig. 3. Rainfall and densities of the Red Locust from December 2005 to May 2008 at Ankiliarivo (hoppers = grey area; adults = black line; rains = histogram). Density scale logarithmic. Monthly tic mark indicates month onset.

dates of arrival of immigrant populations at the onset of the rainy season (sudden increase in adult population densities with no hoppers present during the previous period), maximum hopper and adult densities, date of first hatching, and various indices to help evaluate the mean breeding success as well as the success of embryonic and larval development.

The criteria used are those of Lecoq *et al.* (2006), namely A1 = maximum density of parental adults (n) at the beginning of the rainy season, A2 = maximum density of indigenous (n+1) adults at the end of the rainy season, N = maximum density of hoppers, E = index of egg survival, H = rate of hoppers' survival, R = actual rate of reproduction [population increase from generation 1 (*n*) to generation 2 (*n+1*)], with: E = N/A1, H = A2/N and R = A2/A1. These indices were then correlated with rainfall records, using a multiple correspondence analysis (Escofier & Pagès 1998, Addinsoft XLSTAT software, version 2007.1).

Lastly, for all of southern Madagascar, from September 2001 to August 2007, we constructed a matrix of 7,368 observations and seven variables. The variables corresponded to the densities of hoppers and adults, as well as to the rainfall for the current month n, and for the previous months n-1 to n-4. The correlations between locust data and rainfall were then established by applying to this matrix a co-inertia analysis method (Dolédec & Chessel 1994, Dray *et al.* 2003).

Results

Population dynamics of the Red Locust in the breeding area

In the breeding areas, changes in densities and phenologies of hopper and adult populations, on both the Beomby and Ankiliarivo sites (followed for the former from 2001 to 2003, for the latter from

Table 1. Egg production of the Red Locust at the Beomby site during the 2001-2002 rainy season.

Date	n	Ov	Number of eggs per eggpod		
			1st L	2nd L	3rd L
29 Nov	1	174	-	-	-
18 Dec	11	164 ± 12	87 ± 7	-	-
28 Dec	9	166 ± 4	86 ± 31	-	-
07 Jan	9	164 ± 20	108 ± 15	79 ± 10	-
14 Jan	10	160 ± 28	114 ± 26	113 ± 39	-
21 Jan	4	159 ± 5	97 ± 26	112 ± 17	114
28 Jan	11	157 ± 16	88 ± 20	111 ± 22	70
08 Feb	1	172	116	92	-
Mean		162 ± 17	100 ±25	103 ±28	92 ±31

n: number of females dissected; Ov: number of ovarioles; 1stL, 2ndL, 3rdL: first, second and third oviposition; ± standard deviation.

2005 to 2008) show a succession of biological events repeated from one season to the next with great regularity. The characteristics of each season highlight the critical periods of the biological cycle.

Adult immigration early in the rainy season.—During the dry season in Beomby and Ankiliarivo, hoppers were absent and adult densities very low (<10/ha) (Figs 2, 3). All adults were in sexual (mating) and reproductive (oocyte development) diapause and the primary oocytes remained tiny and translucent in female ovaries (Fig. 4).

At the beginning of the rainy season around October, immigrant populations began to arrive in successive waves. Each wave of immigration corresponded to a rainevent. Thus in Beomby in 2001,

with the first small rains between Oct 9 and 11 (17 mm in 3 d), the adult density increased slightly, passing from 10 to 90/ha between Sep 28 and Oct 12 (Fig. 2). Females in this population were still in reproductive diapause. The end of October was dry and the adult density decreased to 20/ha on Nov 8. A second rainy period occurred on Nov 19-20, with 21 mm of rain. A strong increase in the adult density was immediately noted, with 2,110 adults/ha by Nov 19 (Fig. 2). At this time, the immigrant population ended reproductive diapause and initiated mating and reproductive maturation (*i.e.*, the ovaries initiated oogenesis, with oocytes between 1/4 and 3/4 of their maximum size, and containing yellow yolk). After the Nov-20 rain, a new dry period started that lasted until Dec 16 (Fig. 2). This lack of rain stimulated high emigration, such that the adult density dropped back to 10/ha on Dec 3. Thus, these two first immigrant populations, which arrived at the beginning of the first rains of the season, quickly left the survey site, the environment being undoubtedly too dry and the rainy season not yet well established (Fig. 2).

In December at Beomby, a longer and more intense rain began, and new immigrant adults arrived and remained on the site (Fig. 2). Fairly heavy rain fell from Dec 15 to Jan. 3, 2002 (65 mm on Dec 18, 67 mm on Dec 25, *etc.*). The adult density increased immediately, reaching 4,600/ha on Dec 18. These adults finished their reproductive maturation and laid their eggs locally; the 1st, 2nd, and 3rd layings were observed at the site (Table 1). The adult density then decreased gradually (Fig. 2), probably due to natural mortality in the aging adults. On Jan 24, new rains fell after 3 weeks of dry weather, but the adult density continued to decrease and the population fell to near zero by Feb 7. A similar pattern of arrival of immigrant adults
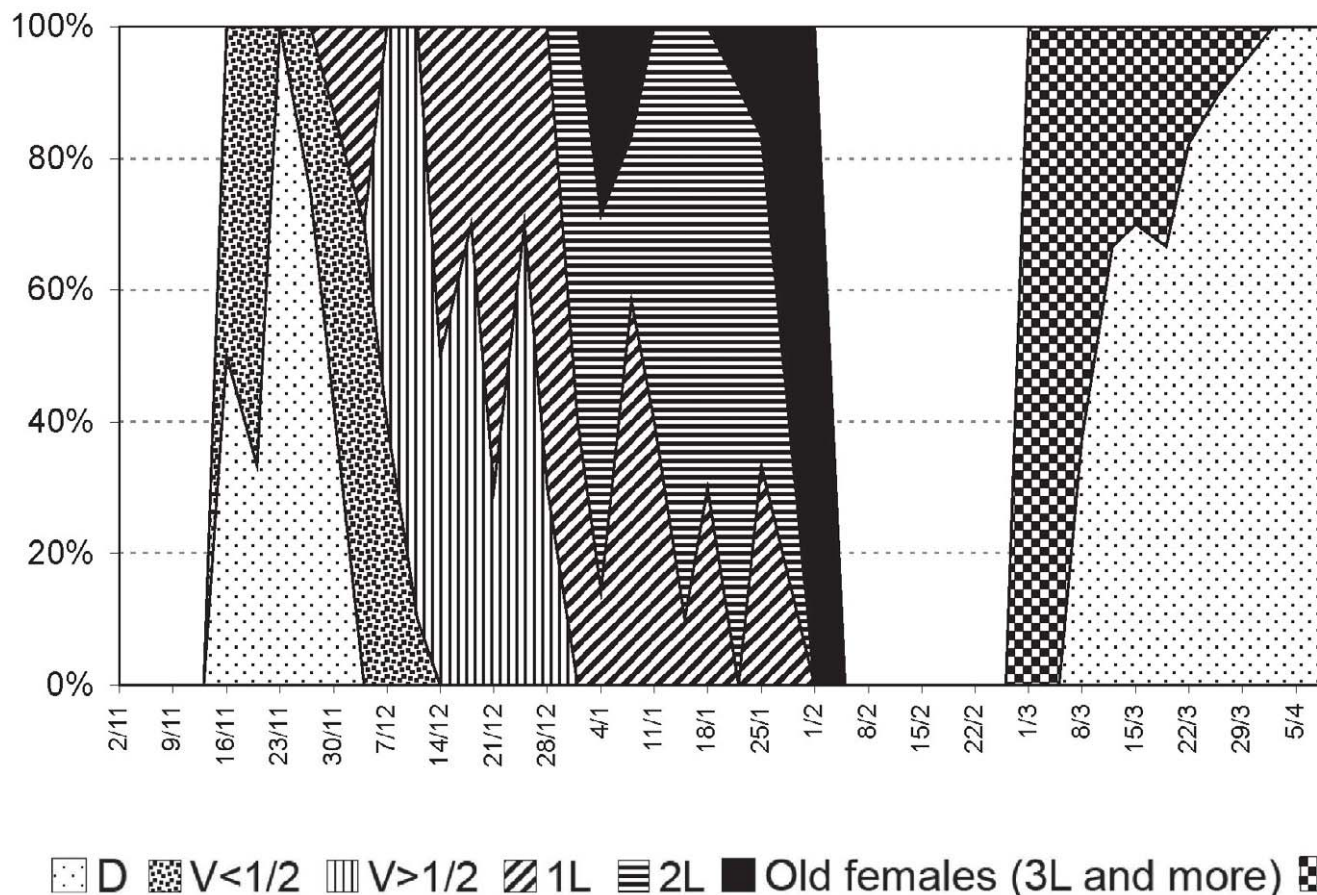

Fig. 4. Female maturation of the Red Locust in 2006-2007 at Ankiliarivo. D = diapause and previtellogenesis; V<1/2 = vitellogenesis, oocytes less than half their final size; V>1/2 = vitellogenesis, oocytes more than half their final size; 1L, 2L = females having laid one or two times; Old females (3L) or more = females having laid three times; F = fledgling (teneral adults).
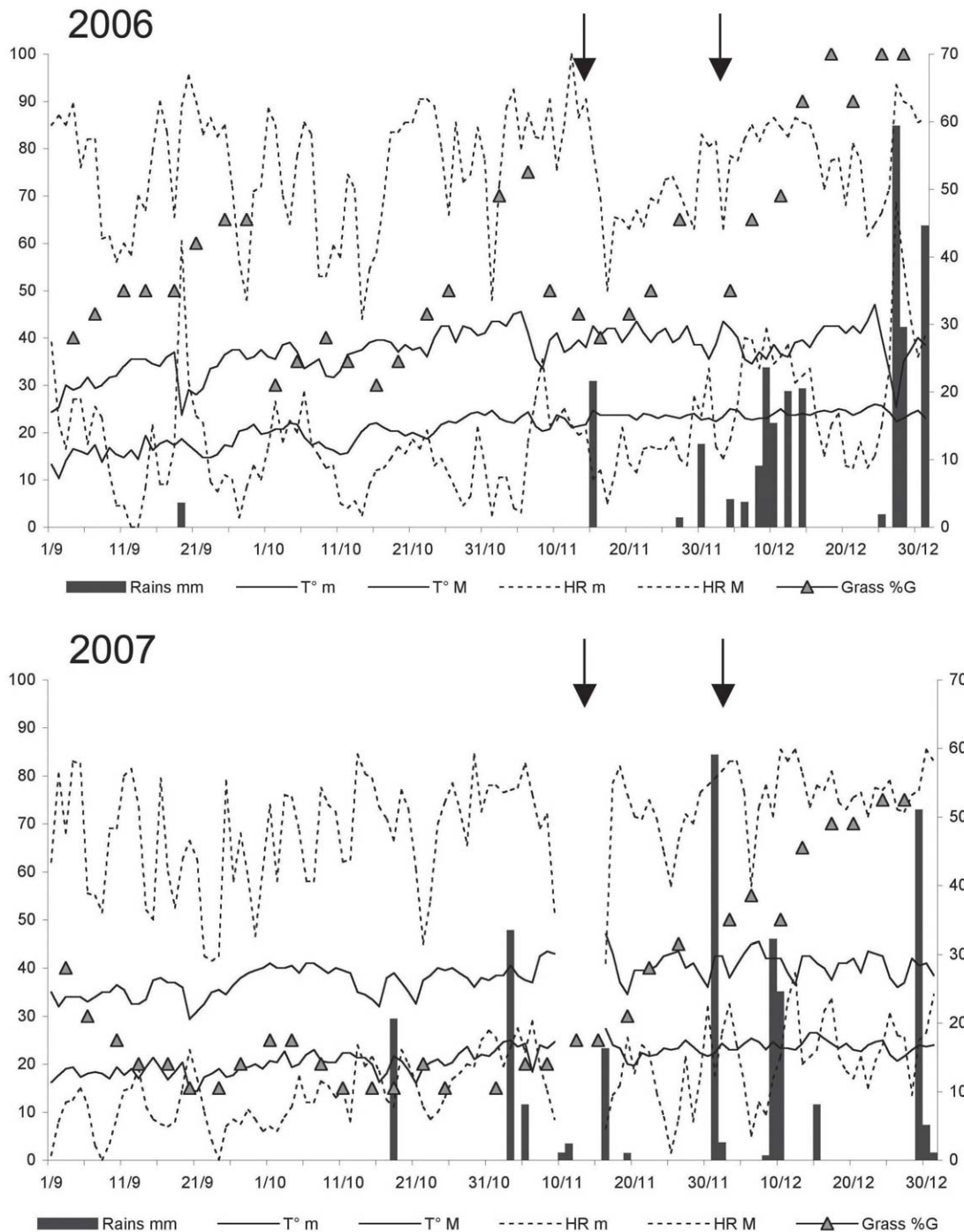
Fig. 5. Temperature, air humidity, rainfall and greenness of grasses at Ankiliarivo 2006-2007 and 2007-2008. Left vertical axis: relative air humidity (HR, min. and max.), air temperature (T°C, min. and max.) and percentage of greenness of the grass (Grass %G). Right vertical axis: rains (histogram: mm). Arrows highlight dates when we observed the first mature females (*i.e.*, first signs of oocyte growth) and the first females that had laid once.

at the beginning of the rainy season was systematically observed each year in our study area (*i.e.*, in Beomby on Nov 11, 2001, if one excludes the small event from October, on Nov 14 in 2002 and in Ankiliarivo on Nov 16, 2006 and Nov 5, 2007) (Figs 2, 3, 7).

Reproductive maturation and laying.—By dissecting females, we determined the beginning of oogenesis (*i.e.*, the breaking of reproductive diapause), the timing of egg laying, and the number of eggs and

egg pods laid. Despite the mixtures of adult populations related to the successive waves of arrivals and departures, and despite high variability in the beginning of the rainy season among years, the beginning of reproductive maturation and the timing of laying were observed each year towards the same dates at both Beomby and Ankiliarivo.

In Beomby, the first females initiated vitellogenesis (V1/4) on Nov 12 in 2001 (with the first significant arrival of adults) and on

Table 2. Breeding success of the Red Locust in the field between 2001 and 2008 at Beomby and Ankiliarivo.

Years	A1	N	A2	E	H	R	Rainfall (mm)			
							Nov	Dec	Jan	Feb
2001-2002	4600	498400	1362	108	0.003	0.30	33	262	75	135
	18/12/01	11/2/02	14/3/02							
2002-2003	810	3900	10	5	0.003	0.01	32	75	98	265
	12/12/02	24/2/03	7/4/03							
2005-2006	1600	51400	1280	32	0.025	0.80	-	131	180	124
	19/12/05	20/2/06	23/3/06							
2006-2007	820	46100	1110	56	0.024	1.35	35	231	161	183
	28/12/06	22/2/07	12/3/07							
2007-2008	1140	45300	1360	40	0.030	1.19	62	184	269	92
	17/12/07	14/2/08	20/3/08							

A1: maximum density of parental adults at the beginning of the rainy season (generation n); N: maximum density of hoppers (generation n+1); A2: maximum density of indigenous adults at the end of the rainy season (generation n+1); E: index of egg survival; H: rate of hoppers survival; R: actual rate of reproduction; Rainfall: quantity of rains at Beomby (2001-2003) or Ankiliarivo (2005-2008); Dates: the dates when the densities were recorded. For A2 only densities of indigenous adults were taken into account and not the densities of immigrant populations.

Nov 14 in 2002. In Ankiliarivo, the beginning of vitellogenesis was noted on Nov 16 in 2006 and on Nov 12 in 2007 (Fig. 4). At Beomby in 2001-2002, females having laid eggs once were noted from Nov 29. Females having laid twice were noted from Jan 7, 2002, and females having laid three times on Jan 21 (Table 1). In Ankiliarivo, in different years, females that had laid their first clutch were first noted on Dec 4, 2006, and Dec 3, 2007 (Figs 4, 5). The first instances of 2nd egg pods being laid were: Dec 26, 2005, Jan 1, 2007 and Dec 27, 2007. Females having laid three times were first observed on Feb 13, 2007 and Feb 4, 2008. Hence, estimated times to complete the 1st 2nd and 3rd gonotrophic cycles were ~ 1 mo, 20 d and 14 d, respectively. At both Beomby and Ankiliarivo, the old adults disappeared by mid-February (Figs 2-4, Table 1). As such, it was rare to find females that had laid more than two egg pods.

Reproductive phenology *of N. septemfasciata* was uniform across years and sites, even though timing of rainfall and greenness of vegetation varied greatly, suggesting that photoperiod and not rainfall, controlled reproductive timing. For example, at Beomby in 2001 the first rains were observed on Oct 9 (17 mm in 3 d), but observed in 2007 on Sept 11 (34 mm) (Fig. 2). At Ankiliarivo, first rains occurred on Nov 15, 2006 (21.5 mm) and then on Oct 18, 2007 (20.5 mm) (Figs 3,4). Temperature, air moisture and vegetation greenness also fluctuated widely from year-to-year (Fig. 5). Hence, reproductive maturation did not correspond to rainfall events, but did coincide to photoperiod changes. In south Madagascar, female Red Locust broke diapause in early November, a time with rapidly increasing day length. At this latitude, day length is shortest in July (10 h, 38 min) and longest in January (13 h, 37 min), with November being around 13 h, after three months of strong increase.

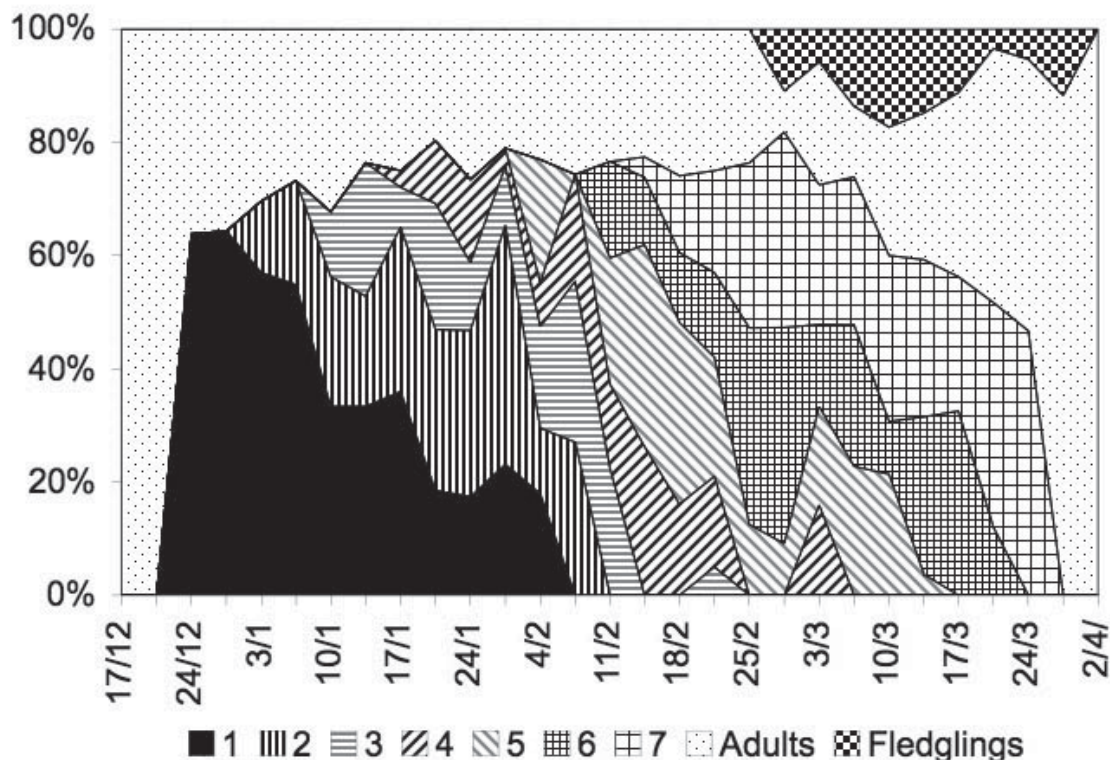At Beomby, during 2001-2002, ovariole number averaged 162 ±

Fig. 6. Hopper development of the Red Locust in 2007-2008 at Ankiliarivo. 1 to 7 = various hopper instars. Adults category does not include fledglings, only adults with hard integuments.
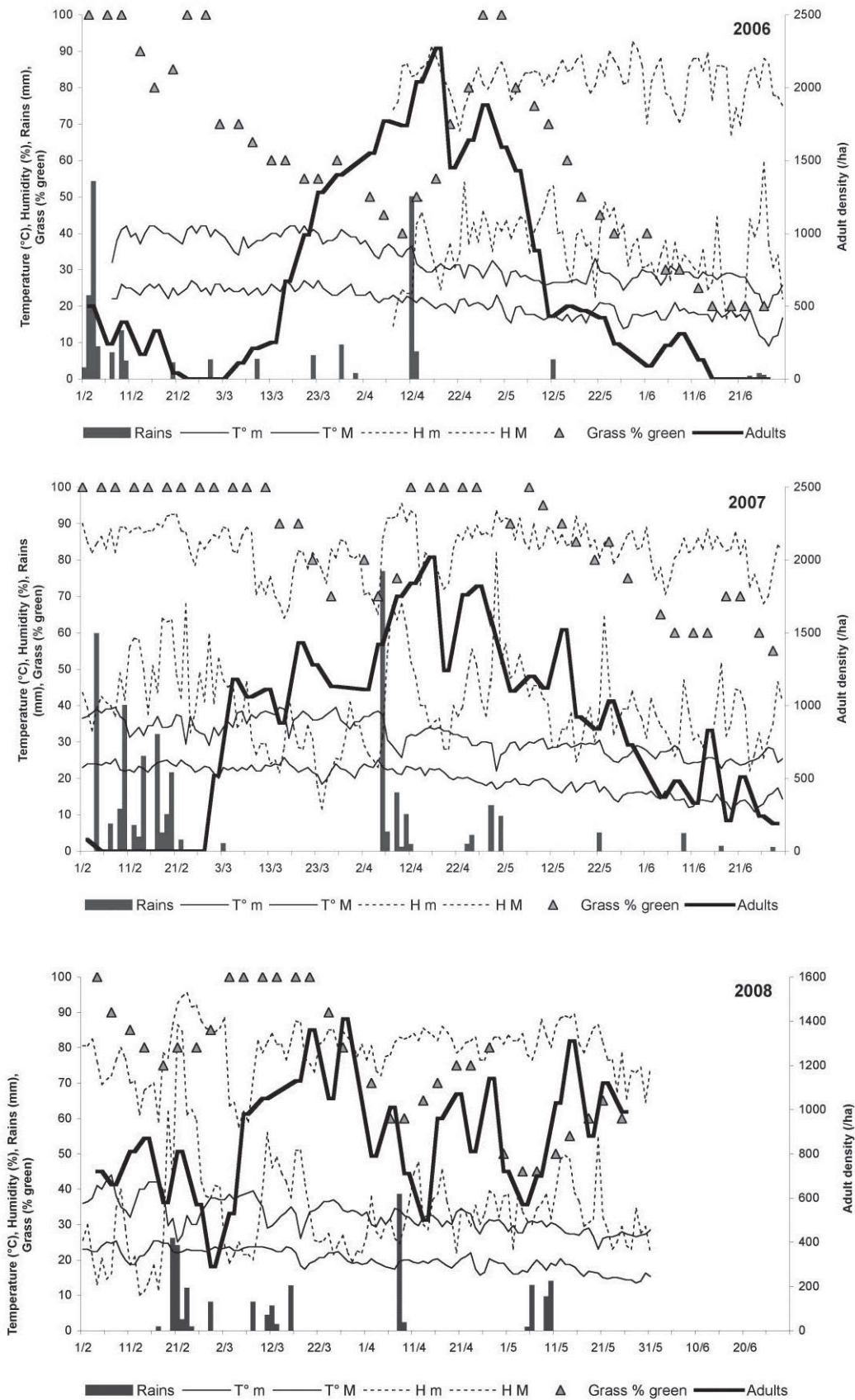
Fig. 7. Ecological conditions and adult density at the end of the rainy season at Ankiliarivo from 2006 to 2008.
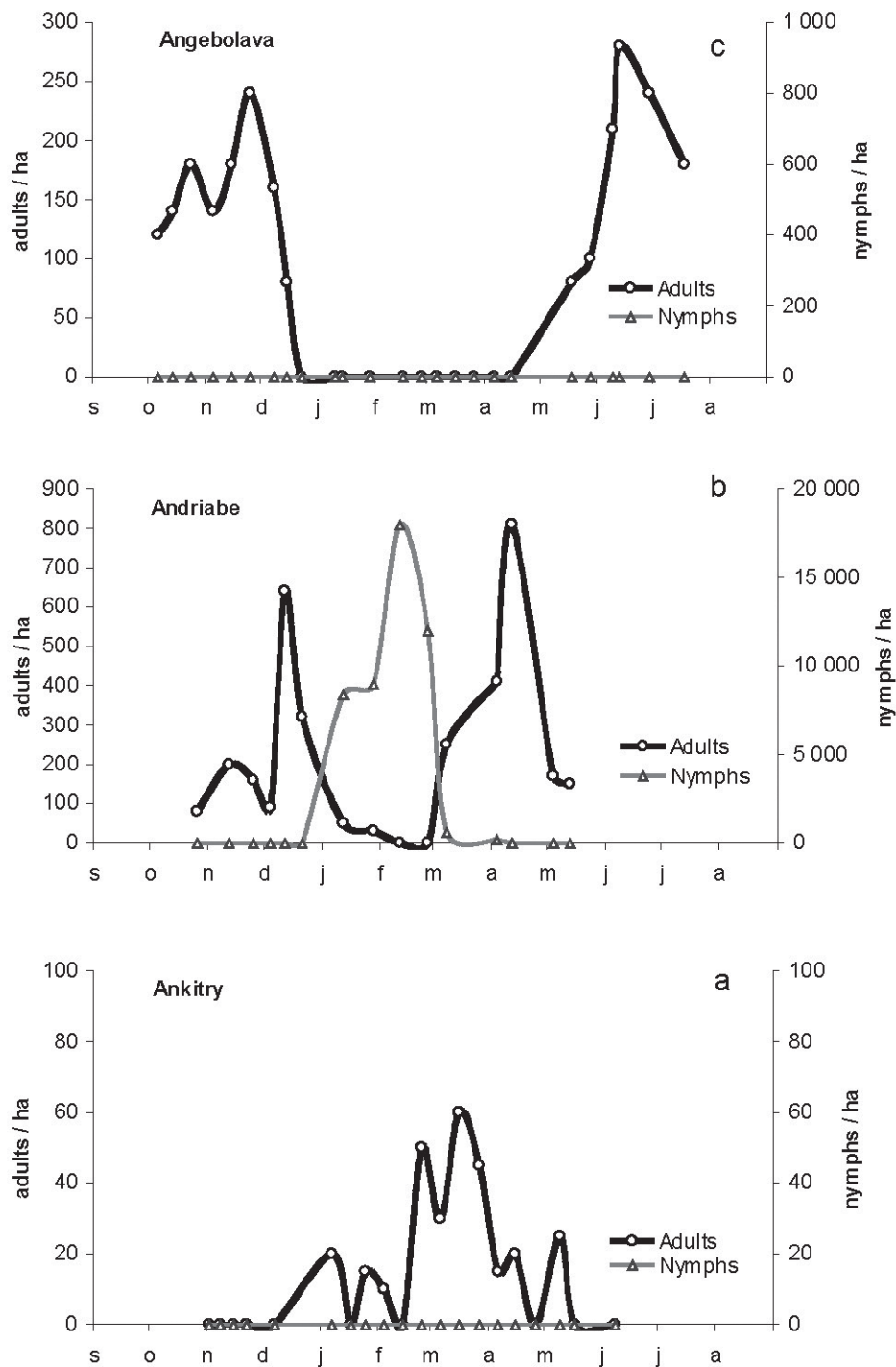
Fig. 8. Evolution of adult and hopper densities in 2005-2006 according to the geographic localisation of the survey sites in southern Madagascar. a) Ankitry (southern limit area, lat 25° 05′18"S, long 46°20′19"E, 110 m). b) Andriabe (breeding area; lat 22°53′22"S, long 44°30′31"E, 3, 444 m). c) Angebolava (refuge area during the dry season; lat 23°36′08"S, long 45°33′02"E, 594 m). See locations on Fig. 9.

17 (Table 1). Mean clutch sizes for the 1st, 2nd and 3rd layings were 100 ± 25, 103 ± 28 and 92 ± 31 eggs respectively. Thus ovarian efficiency (number of eggs/number of ovarioles) for the three gonotrophic cycles are 56%, 73% and 68%. When we examine ovarian efficiency not by egg pod number, but by date (Table 1), we see low ovarian efficiency (around 50%) at the end of December/early January, moderate efficiency (close to 70%) in mid-January, followed by lowered efficiency at the beginning of February, probably due to aging and degradation of females. The adult densities are high at the time of the 1st oviposition, and then drop steadily under the effect of natural mortality (Fig. 2, Table 1). As a consequence, fewer

females take part in the 2nd and even fewer in the 3rd, laying. In 2001-2002, the adult densities were 4,600 adults/ha at the period of the 1st laying, 420/ha at the 2nd and only 15/ha at the 3rd. By multiplying the number of eggs deposited at each oviposition by

Table 3. Breeding success of the Red Locust for the seasons 2004-2005 and 2005-2006 at 72 sites distributed in southern Madagascar (average for all the sites).

Season	E	H	R
2004-2005	18,69	0,13	1,46
2005-2006	1,17	0,02	0,04

E: index of egg survival; H: rate of hoppers' survival; R: actual rate of reproduction.

the density of females taking part in each oviposition, we estimate that ~ 450,000 eggs were laid/ha at Beomby that year (Fig. 2, Table 1). This agrees well with the densities of young hoppers observed thereafter, slightly lower than 500,000/ha. These figures indicate excellent egg survival and hatching.

Embryonic and hopper developments during the rainy season.—Hopper development was observed at about the same dates each year (*i.e.*, between the end of December and the beginning of January). Thus, at Beomby in 2002, the first hatchings and young hoppers of the 1st instar were observed on Jan 7 (Fig. 2). These hoppers resulted primarily from eggs laid after Dec 18. Embryonic development required ~ 20 d (time interval between the first ovipositions and the first hatchlings). Hoppers passed through seven instars and the last hoppers were observed at the beginning of March. The durations of each instar, estimated by a graphic analysis of the field data, was 7, 7, 8, 9, 8, 10 and 12 d from the 1st to the 7th instar respectively, giving a total of 61 d for the whole hopper development in the field.

At Ankiliarivo the duration of the hopper development was estimated at 63 d, based on averaging the 3 y from 2005 to 2008 (*i.e.*, 68, 60, & 60 d). The first hatchings were observed there on Jan 2 for the season 2005-2006, on Jan 4 in 2006-2007 and on Dec 24 in 2007-2008 (Figs 3, 6). Hatching continued during all of January, as a result of spreading out the layings over a long period of time, giving rise to many successive cohorts (see Ankiliarivo in 2008, Fig. 6).

Hopper densities were highly variable from year-to-year according to local ecological conditions. At Beomby in 2002, the maximal density was ~ 500,000/ha on Feb 11 (Fig. 2, Table 2). Starting on Feb 14, hopper density began to fall sharply, reaching < 100,000 hoppers/ha (Fig. 2). This was the result of bush fires lit by farmers on Feb 14 to control the hoppers. In 2003 the hopper density was much lower and did not exceed 3,900/ha (on Feb 24) (Fig. 2, Table 2). Between 2006 and 2008 the hopper densities at Ankiliarivo remained weak and similar from one year to another, at 51,400, 46,100 and 45,300 hoppers/ha (Fig. 3, Table 2).

Fledging and diapausing adults early in the dry season.—At Beomby and Ankiliarivo, the young adults of the new generation appeared each year between mid-March and early April, before the end of the rainy season (Figs 2-4). Adult densities increased over time as more nymphs molted into adults. These adults then hardened their integument and entered sexual and reproductive diapause, with no mating or oocyte development until the following rainy season seven months later. The increase in adult density resulting from the emergence of the young adults lasted for only a short time. Starting in April (a transitional period between the rainy and the dry seasons), the density of adults in the Beomby and Ankiliarivo areas, began to drop, becoming virtually null by the middle of the dry season (July to October) (Figs 2, 3, 7). This was the result of emigration, which corresponded with the environment becoming unfavorable, especially the drying of the vegetation (Fig. 7).

In 2006, between early May and mid-June, the percentage of green grasses declined from 100 to 20%. At the same time, adult density fell from 2,000 adults/ha to none. The same phenomenon was observed in 2007 but more slowly, between the beginning of May and the end of June. In 2008, late rains in April and May caused an irregular drying of the vegetation and the adult density fluctuated correspondingly.

Breeding rates.—Comparisons of the densities of immigrant adults arriving at the beginning of the rainy season (A1), of the densities of hoppers during the rainy season (N) and of young adults of

the new generation at the end of the rainy season (A2), makes it possible to estimate the embryonic (E) and hopper (H) survival, and the rate of reproduction from one year to the other (R) (Table 2). At Beomby, between 2001 and 2003, embryonic survival was very good in 2001-2002 and the population increased by 108×. However, hopper survival was weak, mainly due to bush fires lit by farmers. Overall reproduction was very weak. This was similar to 2002-2003, when both egg and hopper survival was low (Table 2). At Ankiliarivo between 2005 and 2008, egg survival was good, and the population density multiplied between 32 and 56 times. Hopper survival was similar among the three years, ranging between 0.024 and 0.030 (*i.e.*, hopper mortality was between 97 and 98%). As a result, in 2006-2007 and 2007-2008 the new generation had a density slightly higher than the parental generation (1.35 and 1.19 times higher). In contrast, in 2005-2006 the balance was negative, undoubtedly as a consequence of a long dry period from Feb 12 to Apr 12 in the middle of the rainy season.

Regional dynamics of the Red Locust in the south of Madagascar

Biological cycles and their spatial distribution.—At the 72 sites followed regularly by the National Antilocust Centre between 2004 and 2006, the analysis of seasonal changes in hopper and adult densities allowed us to distinguish three main types of biological cycles (Fig. 8). The sites with a Type 1 cycle (Fig. 8a) are characterized by an absence of hoppers during the rainy season, an adult density generally lower than 100/ha (even null on certain sites) and a complete absence of adults during the dry season. During the rainy season, rare adults can be observed from December (adults of generation *n*) to June (adults of the *n+1* generation). If rains are abundant, a small local reproduction is sometimes observed, but generally the resulting hoppers die. On the 72 studied sites, 19 belonged to this category.

The sites presenting a Type 2 cycle (Fig. 8b) are characterized by a low density of adults at the end of the dry season, by arrivals of immigrant adults at the beginning of the rainy season (with a peak of adult density in November and December and densities sometimes largely exceeding 1,000/ha), by hoppers during the rainy season from January to the beginning of April, by a second peak of adults (new generation) at the end of the rainy season (April-May), and by the disappearance (or quasi-disappearance) of the adults in the dry season. Hopper density during the rainy season is highly variable from one site to another and from year-to-year, according to the local ecological conditions; 36 sites are included in this category. This type of cycle is observed in Beomby and Ankiliarivo.

Lastly, Type 3 cycles (Fig 8c) are characterized by an absence of hoppers during the rainy season, adults in diapause in the dry season (often in low densities), a disappearance of the adults early at the beginning of the rainy season (mid-November/early December, when immigrant adults are observed in the sites with a Type 2 cycle) and a re-appearance of immigrant adults in April (when adults in diapause are leaving the sites with a Type 2 cycle). One sometimes observes some hoppers in low densities in these areas, but they fail to survive and no indigenous adults are observed; 27 sites are included in this category.

These three types of biological cycles are organized into three distinct geographical areas, highlighting the spatial and temporal complementarities of the biological events observed in each area (Fig. 9). Type 1 sites occupy a small coastal area of ~ 50 km depth along the entire southwestern coast. This area can be described as "a limit area of the extreme-south", where the annual rainfall is < 40 cm/y, which is insufficient for the development of the Red Locust. Type 2 sites occupy a broad crescent-shaped zone, going from the northwest to the southeast. This zone can be described as a "rainy
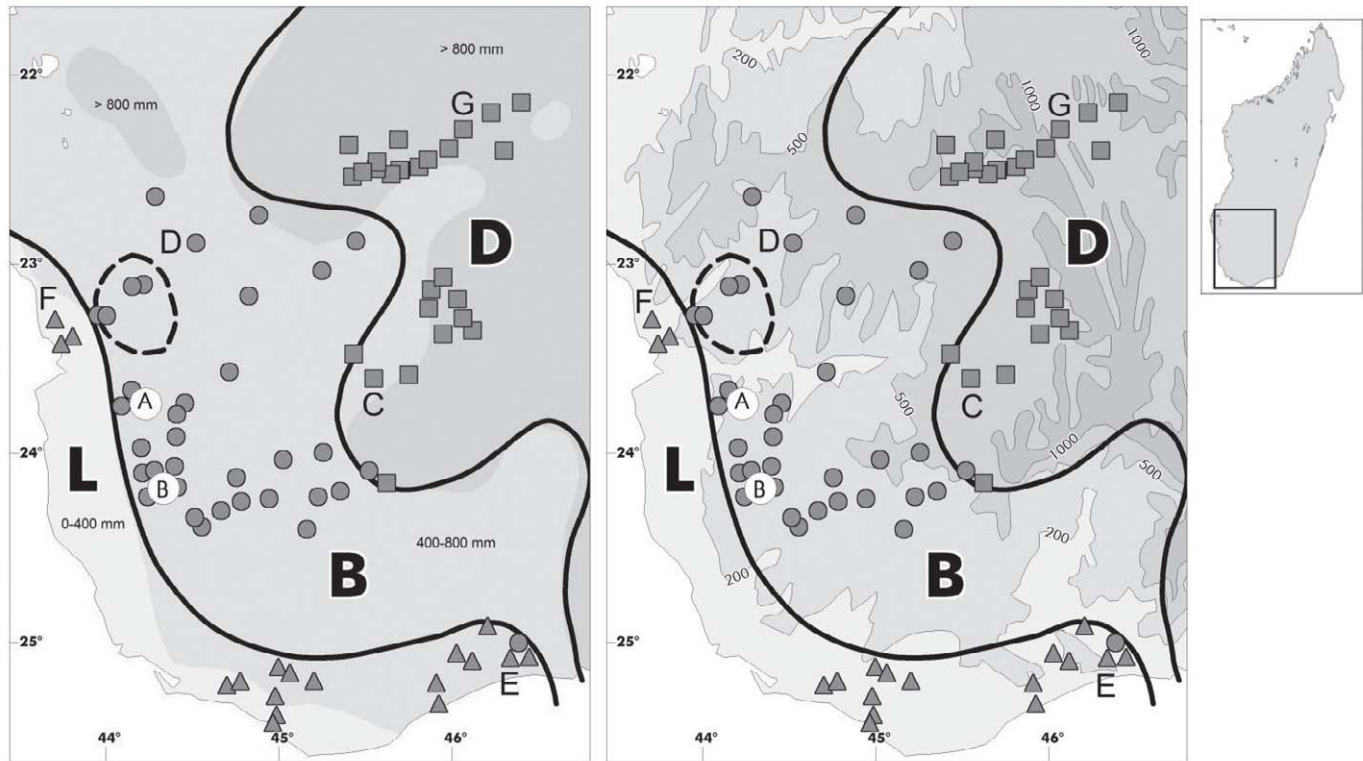
Fig. 9. Biological cycles of the Red Locust in southern Madagascar in relation to rainfall (left) and elevation (right). Synthesis of data from 2004 to 2006. Symbols according to the type of biological cycle: Type 1 (triangle), Type 2 (circle) or Type 3 (square) (see text). Large L = limit area of the extreme-south (less than 400 mm of rains per year); Large B = breeding area (400-800 mm rain); Large D = dry season refuge area (> 800 mm rain). Limits between the three areas take into account the present results, as well as data from Lecoq et al. (2006) (resulting from an analysis of past data from the Antilocust Centre) and surveys of rural inhabitants (Indriambelo 2007). The broken line delimits an area (Belomotra plateau) where important adult populations of Red locust may persist during the dry season for still unknown reasons. Small A = Ankiliarivo; small B = Beomby; small C = Angebolava; small D = Andriabe; small E = Ankitry; small F = Tuléar; small G = Ihosy.
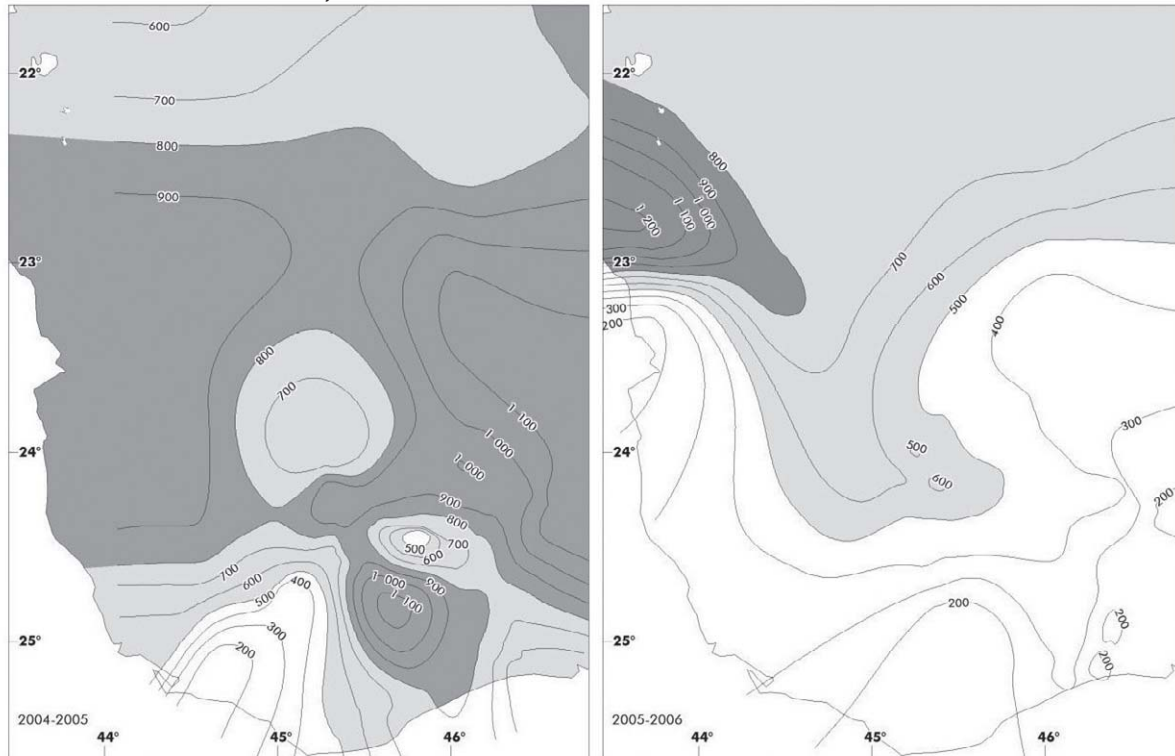

Fig. 10. Comparison of annual rainfall in southern Madagascar in 2004-2005 and 2005-2006.
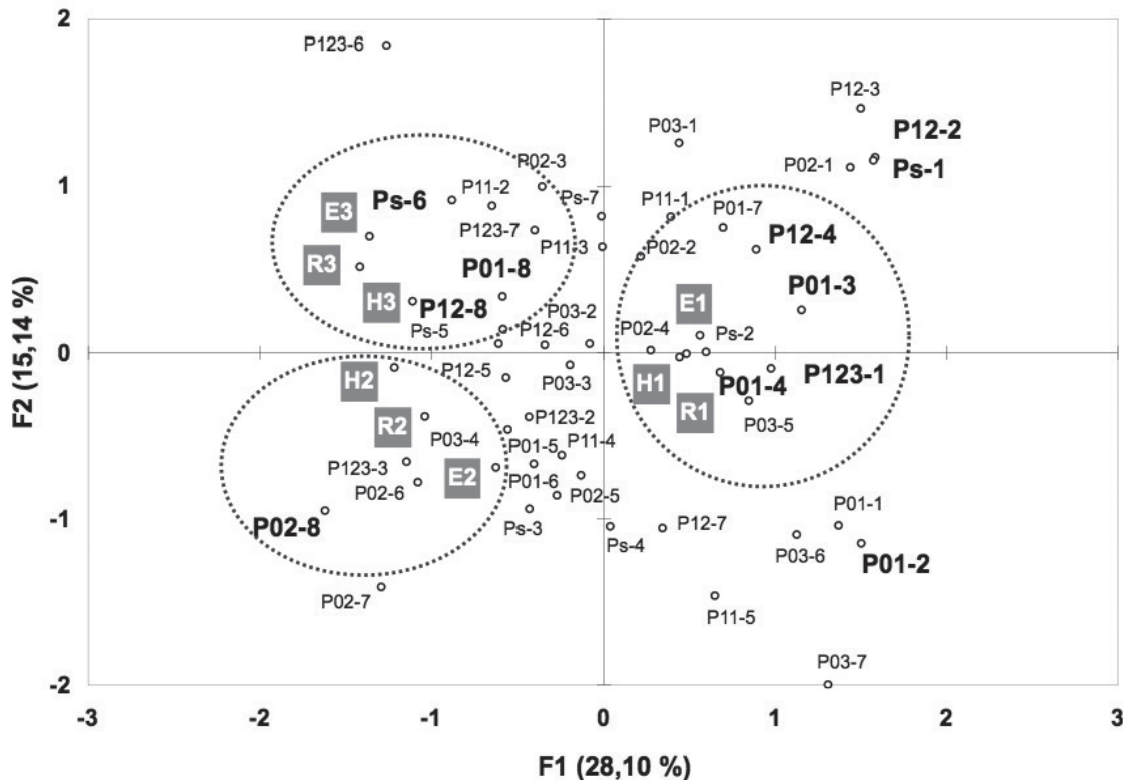
Fig. 11. Multiple correspondence analysis of the table [118 observations × 10 variables]. Only the variables are illustrated here: R = global rate of success for the reproduction from one year to the other (R1 = 0; 0<R2<1; R3 > 1); E = index of egg survival (E1 = 0; 0<E2<10; E3 > 10); H = rate of success of hopper development (H1 = 0; 0<H2<0.25; H3 > 0.25); P11 to P03 = precipitation from November to March (1 < 20 mm; 2 = 20-50 mm; 3 = 50-10 mm; 4 = 100-150 mm; 5 = 150-200 mm; 6 = 200-250 mm; 7 = 250-300 mm; 8 > 300 mm); Ps = total precipitation for the entire season from September to August, and P123 = cumulated rainfall from January to March (1 < 300 mm; 2 = 300-500 mm; 3 = 500-700 mm; 4 = 700-800 mm; 5 = 800-900 mm; 6 = 900-1000 mm; 7 > 1000 mm). All classes were not observed for each variable. Variables in bold or on gray background are those with the strongest contributions to axis 1.

season breeding area", where rainfall lies between 40 and 80 cm/yr. Lastly, Type 3 sites occupy the northeastern part of the study area at the edge of the central highlands, in a zone which can be described as a "dry season refuge area", where rainfall is higher than 80 cm/y, which is apparently too wet for the Red Locust during the middle of the rainy season.

Success of reproduction vs rainfall.—Reproductive success varied among sites and years. For all the studied sites for the 2004-2006 period in southwestern Madagascar, the average egg survival (E), hopper survival (H), and year-to-year rate of reproductive success (R) was higher in 2004-2005 than in 2005-2006 (7.5, 36.5, and 16.0 times greater for the 1st season) (Table 3). In 2004-2005, the index of egg survival was very good (> 10) or good (> 1) in 25 out of 60 sites. The rate of success of hopper development exceeds 0.25 (< 75% of hopper mortality) in nine sites. Lastly, the rate of reproduction is > 1 for 13 sites, indicating that at these locations, Red Locust populations were expanding from one generation to the next. In 2005-2006 only 4 of 68 sites were expanding, and only 15 and 4 sites had, respectively, an index of egg survival > 1 and rate of success of hopper development > 0.25.

These differences in survival and reproductive success between the two years are linked to rainfall; southern Madagascar saw significantly more rain in 2004-2005 than in 2005-2006. For example 98,687 km² received > 80 cm of rain in 2004-2005, but only 10,454 km² in 2005-2006. Conversely, only 6,469 km² received < 50 cm rain in 2004-2005 compared to 68,608 km² in 2005-2006. At a monthly

level, December 2004 and January 2005 were much more rainy in the south than December 2005 and January 2006 (Fig. 10).

To analyze more precisely the relationships between rainfall and reproduction rates, a multiple correspondence analysis was carried out on a disjunctive table [118 observations × 10 variables] (Fig. 11). The 118 observations correspond to the sites on which it was possible (for the seasons 2004-2005 and 2005-2006) to determine the values of the rates of reproduction. The 10 variables correspond with the rates of reproduction (3 variables: E, H and R), the precipitation from November to March (5 variables: P11, P12, P01, P02, P03), the total precipitation for the season (1 variable: PS) and the cumulated rainfall from January to March (1 variable: P123). Each variable was transformed into classes according to the limits indicated in the legend of Fig. 11. The first two factorial axes gather 43% of the inertia.

Axis 1 (28.10% of inertia) separates the sites where a zero value for the rate of reproduction was observed (class 1) from those presenting positive values (classes 2 and 3). The strongest rates of reproduction are associated with strong rainfalls (over 30 cm/month) in December (P12-8), January (P01-8) and February (P02-8), as well as with an important total rainfall from September to August (PS-6) ranging between 90 and 100 cm. Low rates of reproduction are associated with low rainfall for December and January, as well as with low values of total rainfall for the whole season (< 30 cm/year) and of cumulated rainfall from January to March (< 30 cm).

Axis 2 (15.14% of inertia) separates the sites with high reproduction (class 3) from the sites where the rates of reproduction
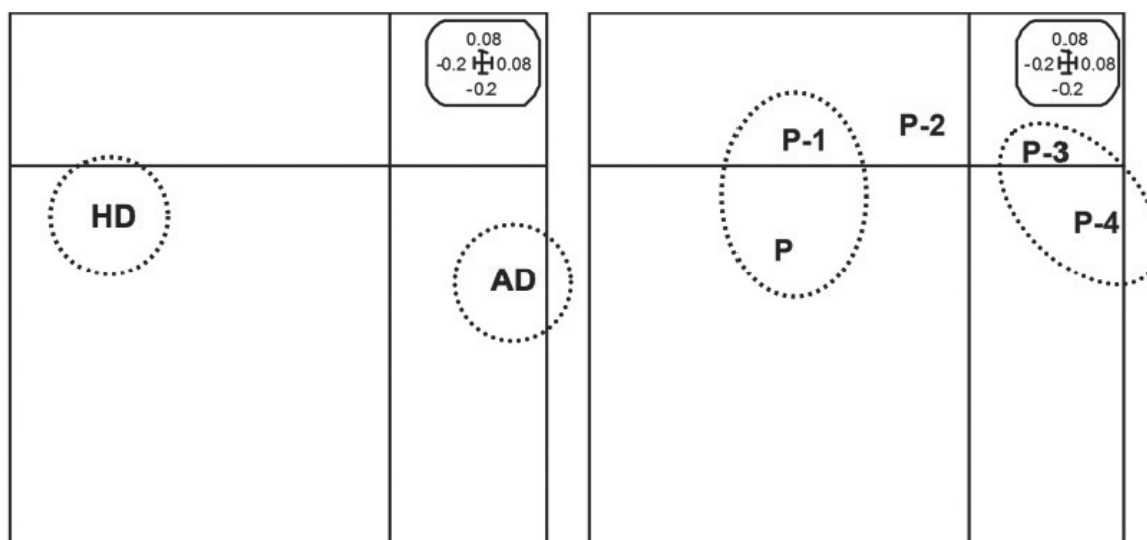
Fig. 12. Co-inertia analysis of the matrix [7368 surveys × 7 variables (2 locust variables + 5 rainfall variables)]: representation of the variables on the plane defined by the first two factorial axes. The densities of hoppers and adults are represented on the left graph, rainfall on the right. These two factorial planes were created by the co-inertia analysis and thus can be read simultaneously. The HD variable (hoppers density), whose negative factorial value on the first axis is the highest, is strongly correlated with the variables P and P-1 (rainfall of the current month and of the previous one) which are in the same situation on the factorial plane for the rains distribution. On the other side, AD (adult density) is negatively correlated with P and P-1 and positively, but slightly, with P-3 and P-4.

are low (class 2). It opposes, in particular, the sites having a high index of egg survival (strong contribution of E3 on the positive side) to those where this index is low (strong contribution of E2 on the negative side). The high values of the index of egg survival (class 3) are associated with the very strong rainfall values (more than 30 cm/month) of December and January (P12-8 and P01-8), as well as with a strong annual rainfall (PS-6: 90-100 cm/y). The intermediate values (class 2) are associated with weaker rainfall levels of P12 (5-6-7: 15-30 cm), P01 (5-6: 15-25 cm) and PS (3-4: 50-80 cm/y).

On all the available data for the period 2001-2007, the analysis of co-inertia realized on the matrix [7368 observations x 12 variables] highlighted a strong positive correlation between hopper densities and the rainfall values of months n (P) and $n-1$ (P-1) (Fig. 12). The higher the rainfall during the current month, and during the previous month (between January and April), the higher the resulting hopper densities on the breeding sites. However, above 30 cm of rainfall, the average density of hoppers drops slightly and the ecological conditions seem less favorable.

This hopper density is negatively correlated with P-3 and P-4 (rainfall 3 and 4 months earlier), which seems logical and in agreement with a hopper development of about 2 months. For the adults, density is positively correlated with P-3 and P-4. One can see here the influence of December, November, and January rainfall on the success of the embryonic development and, consequently, on the density of the adult population of the new generation appearing between March and April in the breeding area. On the other hand, adult density is strongly negatively correlated with rainfall of months n and $n-1$.

Discussion

This paper describes the life cycle, phenology, reproductive diapause, and migration patterns of the Red Locust, *Nomadacris septemfasciata* (Serville) in southern Madagascar. We show that the biological cycle of the Red Locust repeats each year with great regularity. We also identify the most favorable zones for gregarization,

and examine the population dynamics, quantifying the impact of ecological conditions on the rate of reproduction. Based on this eight-year study, we propose new strategies to control this pest in southern Madagascar.

Migrations.—Our study of the biological cycle of the Red Locust in south Madagascar shows the importance of the seasonal migrations. The three types of biological cycles observed in the south are clearly complementary, with annual movements mainly between dry-season refuge areas and wet-season breeding areas. Such seasonal migrations for the Red Locust were long suspected (Têtefort & Wintrebert 1967, Randrianasolo 1978). Our current findings reinforce the conclusions of preceding work carried out on the basis of an analysis of old archives of the Malagasy National Antilocust Centre, and information gathered from local farmers (Lecoq *et al.* 2006). At that time, we distinguished five main areas: refuge area for the dry season, transitory area, main and secondary breeding areas, and limit area along the extreme south. Now we propose only three primary areas, and more precisely define and delineate them, based on our extensive 2001-2008 dataset.

Our work shows that the seasonal migrations are related to rainfall conditions as previously suggested (Lecoq *et al.* 2006). The adults migrate towards the south in October and November, at a time when the rainy season becomes established gradually and when monsoon winds bringing the rains, lead the insects towards the south and the breeding area. The adults may be driven out by excess moisture, as has been demonstrated for the Migratory Locust in Madagascar and Africa (Launois 1974; Lecoq 1975, 1995) and for the Senegalese Grasshopper in West Africa (Launois 1978, 1979; Maiga *et al.* 2008). These solitary movements likely take place at night, as is the case for Migratory Locusts (Lecoq 1975, Farrow 1990) and Desert Locusts in Africa (Roffey 1963, Popov 1969). The arrivals of adults in the southern breeding area coincide strictly with the various periods of rains at the beginning of the rainy season. Each rainy period is accompanied by an arrival of immigrant adults which leave the area quickly if the rains in that particular area do not continue. The return migration of the young diapausing adults

from the south to the north in April and May, coincides with the end of the rainy season, the desiccation of the vegetation, and the change in wind direction, which blows from south to north during the dry season. This favors the northward displacement of the adults towards the refuge area, where they remain until October and November.

In Africa, the Red Locust is fairly well studied in its outbreak areas, and the movement patterns of gregarious individuals are well documented (Morant 1947, COPR 1982, Bahana 1999). However, little is known about the flight patterns of solitary Red Locusts (Golding 1934; Burnett 1951; Descamps 1953, 1965; Chapman 1959; Davey *et al.* 1959), including the long-distance movements of solitary Red Locusts in their outbreak areas in Africa (Lecoq *et al.* 2006). In Madagascar, such seasonal migrations recall those of the Migratory Locust, *L. migratoria*, the main pest locust on the island. In Madagascar, *L. migratoria* has four generations a year, and undertakes major migrations throughout the year in relation to the displacement of the zones receiving between 5 and 15 cm of rain per month (Launois 1974; Lecoq 1975, 1995). At the beginning of the rainy season, these migrations are directed to the south, and at the beginning of the dry season, towards the north. Such migrations of solitary populations can concentrate adult *L. migratoria* at the beginning of the rainy season, and lead to gregarization and outbreaks in Madagascar (Lecoq 1975).

It is certainly the same for the Red locust, where the migration towards the south at the beginning of the rainy season increases sharply population density in the breeding area, compared to the low densities that exist in the refuge areas during the dry season. On average, adult densities change from about 100/ha in the refuge area to 1,000/ha at the beginning of the rainy season in the breeding area in the south of Madagascar. However, the fact that the Red Locust only has one generation per year reduces this species' potential for rapid population response to irregular rainfall conditions, which could partially explain why Red Locust outbreaks are less common and smaller in comparison to those of Migratory Locusts (Lecoq *et al.* 2006). Other factors should also be taken into account, especially the higher gregarization threshold, *i.e.*, around 5,000 adults/ha for Red Locusts *vs* 2,000 adults/ha for migratory locusts (Franc *et al.* 2005).

Diapause.—The adult life of the Red Locust is marked by a long period of adult sexual and reproductive diapause during the entire dry season (May-November). Norris (1959a, 1959b, 1962, 1965) has shown that this imaginal diapause is induced by a short photoperiod operating during the adult stage, in spite of the low latitudes normally inhabited by this species. In the laboratory, the critical constant day-length for inducing and maintaining diapause lies between 12 and 13 h (Norris 1959b). This range matches the maximum and minimum day-lengths at 7° N or S latitude. Thus, it is probable that day-length is responsible for the onset of diapause in the field in Madagascar: diapause induction must be triggered by decreasing photoperiod at the time of the emergence of the young adults in March/April.

For the termination of diapause, we did not find a direct correlation between rains and the beginning of vitellogenesis, as was suggested previously by some authors (Robertson 1958, Norris 1965, Franc & Luong-Skovmand 2009). Our study shows that in south Madagascar, the beginning of the rainy season and the quantity and distribution of rain was highly variable from year-to-year, yet the dates of locust life-history events were relatively constant from year-to-year. Thus, our results strongly suggest that photoperiod is the factor that ends diapause and initiates oogenesis in females, and not rainfall, temperature or food.

Dates for the beginning of vitellogenesis and the 1st and 2nd egg pods were especially constant across years. At the time of diapause termination and reproductive maturation, day-length at the latitude of our study is increasing rapidly (42-min increase in October and 43-min increase in November). The total annual range of day-length fluctuation is 2 h and 59 min between January and July. Thus, we disagree with Franc and Launois-Luong (2009) who suggest that photoperiod "*may not play a large role in reproductive maturation, because their area is situated close to the Equator (15° S) where photoperiod is relatively constant*" and that "*rain is required to trigger rapid vitellogenesis*".

Actually, even in the northern tip of Madagascar (closest to the Equator), the duration of the light period varies almost 2 h (1 h and 47 min) during the year, whereas even 55 min fluctuation in photophase-length is sufficient to induce diapause (Norris 1965). The related Bombay Locust (*Nomadacris succincta*), also uses daylight-length as a cue to control the time of adult diapause termination in the field, and uses a similar threshold value (L:D 14:10) as that observed for *N. septemfasciata* in south Madagascar (L:D 13.37:10.23) (Tanaka & Sadoyama 1997).

Our results also differ from those of Robertson (1958) in Rukwa valley in Tanzania, who showed that in *N. septemfasciata* "*vitellogenesis onset is correlated with a fall in maximum temperatures, consecutive to a medium or heavy rainfall*" and of Norris (*loc. cit.*), who stresses that "*the timing of this vary [sic] among years, probably because the termination of diapause depends on temperature and moisture, which are variable*".

Albrecht (1956) also highlights a population synchrony in laying for the Red Locust; he attributes it to the abrupt change in climatic conditions and to the sudden appearance of the rainy season, which causes the termination of adult diapause simultaneously for all the individuals of the population. Actually, it seems that the rains will simply modulate, not the speed of the events, but the mortality rate of the various cohorts concerned, in particular egg survival. Of course increased day-length coincides with both increased rain and the arrival of adults in the breeding area, and this makes it difficult to determine the causal factor.

Rate of oocyte development, oocyte resorption, and egg survival.—Our data suggest that increased photoperiod acts to terminate reproductive diapause in adults, triggering both mating and oocyte development in females. However, once oocyte development begins, three other environmental factors (rainfall, temperature and nutrition) may determine its subsequent rate of progression and success (Hodin 2009). Intermittent or insufficient rains can delay or reduce new plant growth, lower plant nutritional value and thereby slow or stop grasshopper oocyte growth (Stauffer & Whitman 1997). In addition, females can resorb their developing primary oocytes when nutritionally stressed (Lecoq 1975, Sundberg *et al.* 2001). The number of oocytes resorbed corresponds to the severity of the stress: under mild nutritional stress a few of the developing oocytes may be resorbed, whereas under severe starvation all primary oocytes can be rapidly resorbed (Launois 1972). Hence, when there is no food, the 1st gonotrophic cycle may be totally nullified in some species. Unseasonably low temperatures or cloudy conditions (which reduce solar-heating) can also slow oocyte development, delaying oviposition (Stauffer & Whitman 1997). Together, rain, temperature, and plant quality can speed or delay oocyte development and egg laying, once reproductive development is initiated via photoperiod.

Nevertheless our results show that when oocyte development starts in mid-November, the vegetation is generally never completely dry, even when rains are late or inconsistent. For example, in 2006 and 2007, vegetation greenness in mid-November averaged 30%

and 20% respectively, resulting either from the first rains, or from the bush fires of the dry season having stimulated the regrowth of green vegetation and thus provided the nutritive resources necessary to the Red Locust for its breeding activity. Hence, it is probable that in south Madagascar females usually find conditions more-or-less acceptable for oocyte maturation and laying (even if ovarian efficiency may vary according to ecological conditions). However, even if large numbers of eggs are laid, poor rains can dry the soil and kill most of the eggs. Thus, unfavorable ecological conditions can destroy entire cohorts of egg pods, giving the impression that "*the timing of this vary [sic] among years*", according to the expression of Norris (1965).

Hence, in south Madagascar, reproductive diapause is terminated by photoperiod on a fixed date each year. However, the timing and success of subsequent oviposition varies from year-to-year and place-to-place due to local variation in rainfall, temperature, and plant quality. This same process occurs in *Rhammatocerus schistocercoides* (Rehn 1906), a pest locust in Brazil. There, sexual maturation is triggered by photoperiod on a set date, but then progresses under highly variable ecological conditions (Launois-Luong & Lecoq 1996).

Rainfall and reproductive rate.—Rains greatly impact grasshopper reproductive success (Symmons 1959, Joern & Gaines 1990, Stauffer & Whitman 1997). Comparison of the reproduction rates observed in south Madagascar, as well as annual comparison of these same rates on a same site, demonstrates the strong impact of the abundance and distribution of the rains on both egg and nymph survival, eggs and nymphs seeming to constitute critical periods of the biological cycle of the Red Locust. Low or badly distributed rainfall at the beginning of the rainy season can cause partial or complete egg mortality in a given area. Likewise, both long dry periods and excessive rainfall can greatly reduce hopper survival. Our data suggest that a minimum of ~ 15 cm of rain per month is needed for successful egg development.

Beyond that, more abundant and well-distributed rains in the breeding area greatly increase the rate of reproductive success and the risks of an outbreak. Only a monthly rainfall higher than ~ 30 cm seems to become unfavorable, reducing slightly overall egg survival. Rainfall > 40 cm/month clearly decreases Red Locust density. Franc *et al.* (2005) noted, for Madagascar, that the intercalation of dry periods during the rainy season caused egg mortality and as a consequence, very low rates of reproduction (even null), whereas a regular distribution of the rains allowed rapid population growth. The key periods for reproductive success are the egg stages. In Africa, many authors also showed that the egg stage is the weak link in the biological cycle of the Red Locust and that the intercalation of a dry period after the first laying is a key mortality factor (Du Plessis 1937, 1938; Lea & Webb 1939; Albrecht 1956; Gunn 1956; Hemming 1964). Such is also the case in Madagascar and lessons can be drawn for the management of this pest.

Improved locust management.—Our findings may aid Red Locust control by the Malagasy National Antilocust Centre. Our study shows that in southern Madagascar, the Red Locust primarily breeds along a narrow southwestern edge, at the northeastern limit of the dry forest. This area (extending from Befandriana-Atsimo to the Mahafaly plateau and including the plateau of Belomotra), is particularly favorable for outbreak and gregarization, because it receives good rainfall, has high rates of immigration at the beginning of the rainy season (favoring a sudden concentration of solitary populations in restricted areas which can stimulate gregarization), and high rates of egg and nymphal survival (Lecoq *et al.* 2006). Intensive defor-

estation (for crops, charcoal, timber *etc.*) during the last 20 y has also created new favorable habitats for the Red Locust in this area. Finally, this zone tends to have more tertiary limestone areas and heavier soils, which favor egg survival; other areas tend to possess sandy soils which dry and desiccate eggs.

Based on the above information, we recommend the following management strategies for the Red Locust in southern Madagascar:

1. Increase surveys in the main outbreak area, mainly at the beginning of the rainy season, to better assess the locust situation (this zone is currently not well surveyed by the Antilocust Centre).

2. Better monitored rainfall at the beginning of the rainy season (December and January) and in areas with > 15 cm rain/month (with special attention to the main outbreak area and to the rainfall range 25-30 cm/month, which seems the most favorable for the Red Locust). On-going analysis of the temporal distribution of the rains should facilitate accurate risk prediction at each site. In general, more uniform rain distribution increases risk. In contrast, dry periods of more than three weeks reduces risk.

3. Close monitoring of deforestation, since forest loss can create new habitats for successful breeding.

By using the above strategies, we believe that the Red Locust can be successfully controlled in south Madagascar. Firstly, we have identified the primary breeding zones and weather factors that favor successful breeding and outbreak. Secondly, the Red Locust has only one generation a year (in contrast to the Migratory Locust with 4-5 generations). Hence population increase and gregarization (which can lead to invasion) are relatively slow. This should allow the NAC to focus on a smaller geographic area (the primary breeding zones) and also on those weather factors that stimulate outbreaks.

Finally, the annual cycle of this pest insect allows more time to monitor and possibly control the situation at an early stage. This strategy should allow the NAC to prevent most large outbreaks and massive invasions. However, the Red Locust also has a tendency for frequent small and local outbreaks. The NAC will need to continue to provide locust-control assistance at the farm and village level, as well as to combat large outbreaks and invasions of this crop pest.

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