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Not a one-way trip: historical distribution data for Australian plague locusts support frequent seasonal exchange migrations

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Abstract

An analysis of the development of infestations of the Australian plague locust (*Chortoicetes terminifera*) (Walker) (Orthoptera: Acrididae) from 1977-1995 in eastern Australia is presented which traces the sequence of generations and redistribution of gregarious populations through migration. Migration in this species has previously been viewed as a one-way trip, locusts reaching southern regions of the species range were thought to have no reliable means of return to the areas of summer population increase in western Queensland. However, a study of outbreaks over recent years, using new technologies for simulating and observing migratory events, suggested a pattern of exchange migrations, with northward movements in November and December.

In this paper we provide further evidence of migrations to western Queensland from populations in the southern or eastern parts of the species range. Several northward or westward migrations from New South Wales, South Australia or eastern Queensland are identified from historic distribution data and supported by meteorological records. These migrations were significant in that they allowed the rapid re-establishment of gregarious populations in arid western Queensland after summer rains. The frequency of late-spring northward migrations is comparable to that of the better-known southward migrations in autumn. The evidence for previous conclusions about the source of historical plagues and the importance of spring breeding in arid southwest Queensland are re-examined in the light of these findings.

Key words

Chortoicetes terminifera, locust, Australian plague locust, migration, outbreak history, plague development

Introduction

The Australian plague locust (*Chortoicetes terminifera*) (Walker) (Orthoptera: Acrididae) is a frequent agricultural pest in Australia, with mass migration contributing to the geographic expansion of infestations. Successful breeding of a summer generation in western Queensland (Qld), followed by large-scale autumn migration of populations into agricultural and pastoral areas of New South Wales (NSW), South Australia (SA) and Victoria, has been important in the development of many major pest infestations. Another common feature of those infestations was widespread heavy summer rainfall in the arid inland that enabled large intergenerational population increase. At these times the normally sparse grassland and herb-field habitats of southwest Qld provide an enormous area of temporarily abundant resources.

The lifecycle and migratory behavior of *C. terminifera* have been studied in some detail (Clark 1965,1969,1971,1972; Farrow 1975,1979; Hunter *et al.* 1981; Hunter 1982). There are typically 2 or 3 generations from spring to autumn across the geographic range of the species. Eggs may suspend development in a quiescent state in dry conditions and egg diapause operates to inhibit development over the winter months (Wardhaugh 1980, Hunter & Gregg 1984). After fledging, immature adults pass through a stage of fat accumulation followed by a peak in migratory behavior. One, of potentially multiple, egg-development phases follows or is coincident with these migratory phases. Pre-reproductive adults often undertake wind-assisted long-distance nocturnal migratory flights, that can displace populations hundreds of kilometers. Migratory flight may continue over a number of days and migrations may be repeated between egg layings (Clark 1965). Take-off occurs over a series of nights above a temperature threshold of 20°C (Clark 1969, 1971), but there is an association of major migrations and large displacements with disturbed weather such as low-pressure troughs or frontal systems (Clark 1969; Farrow 1975, 1979). These movements may result in widespread dispersal or in convergence and aggregation. Rainfall events are a major synchronising force in locust reproduction, gregarisation and migration, but asynchronous generations and a range of ages is common in field populations.

The last published discussion of migrations of *C. terminifera* in relation to the development of major outbreaks was that of Wright (1987). In that study 6 major infestations between 1934 and 1984 were identified as plagues and the sequence and location of the generations contributing to each were reconstructed. Plagues of this species last 1 to 3 y and were differentiated from more frequent infestations by the extension of high density populations of adult swarms and nymphal bands across the inland agricultural regions of several Australian states. The major conclusion drawn was that 5 of those 6 plagues originated in the arid interior of eastern central Australia in the region centered on the Channel Country of southwest Qld — the plague source area (Fig. 1). While there has been some recent reference to the complexity of migratory movements for the species (Hunter *et al.* 2001; APLC 1992, 1995), this paper examines all data from the last 25 y and addresses the fundamental premise of the 'arid source area' model.

Wright's paper was significant in that it provided evidence of late summer and autumn migrations of swarms into agricultural areas from more northerly inland areas as a common feature in major pest outbreaks of *C. terminifera*. It was the first analysis to attempt to reconstruct the relevant environmental conditions during outbreak development (rainfall, temperature, plant growth, upper-level winds) and to match these to historical records of locust distribution and

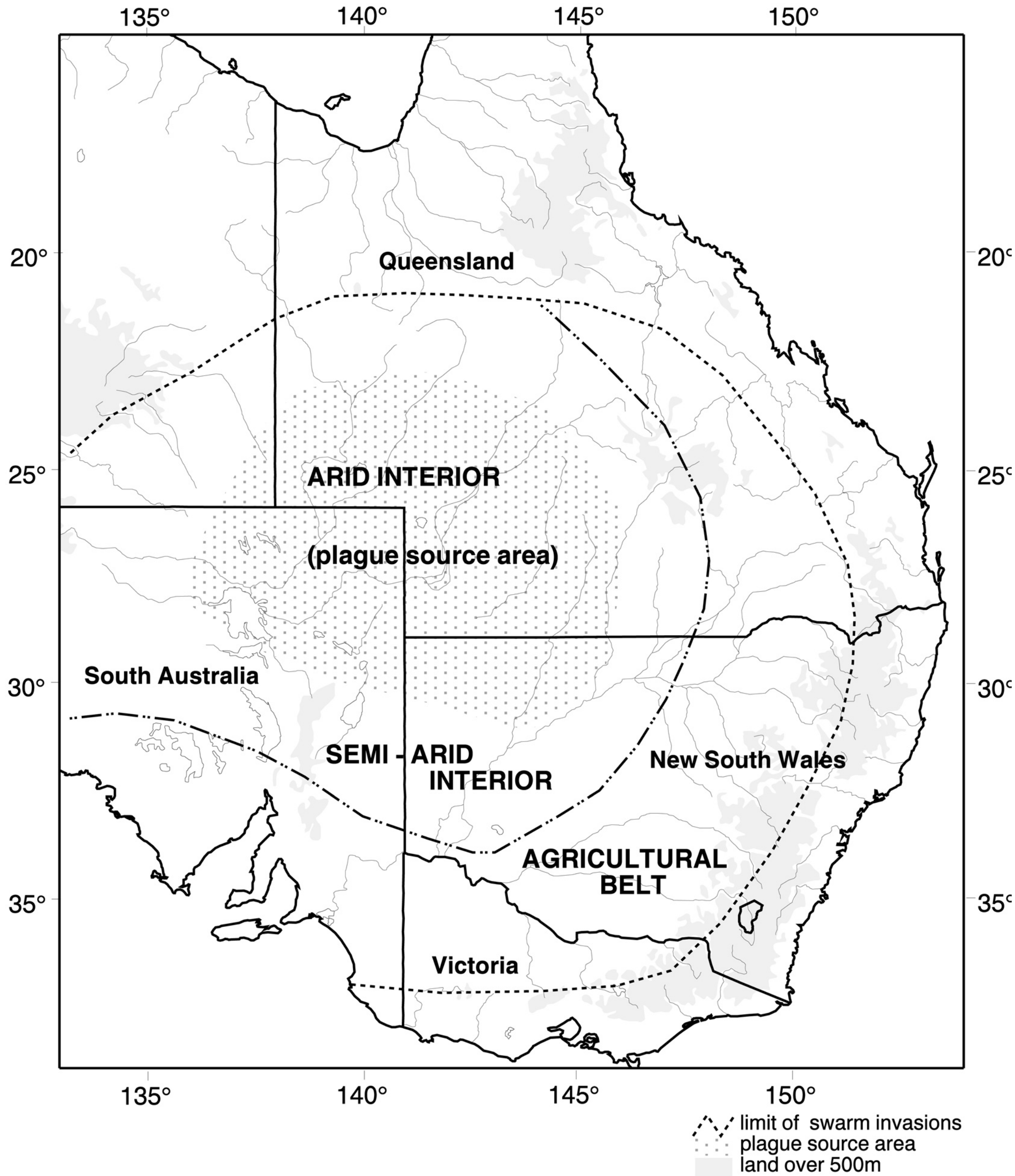

Fig. 1. Plague source area (redrawn from Fig. 2 of Wright 1987).

critical development times, determined by a specific phenological model for the species. It was also an influential paper in terms of subsequent approaches to forecasting and control strategy within the Australian Plague Locust Commission (APLC) and to the migratory ecology of the species. It remains the most frequently cited reference dealing with migration in this species and it established the conceptual model of plagues originating solely from a sequence of breeding in one part of the arid inland (Symmons 1984; Bryceson & Wright 1986; Morton 1996; Hunter 1986, 1989; Farrow & Drake 1991; Hunter *et al.* 1996, 2001). That model was in part based on an assumption that there is no reliable means of return migration to the inland (Wright 1983, Symmons & McCulloch 1980, Symmons 1986); spring breeding within the 'plague source' area was therefore seen as critical to the establishment of the large summer populations there (Wright 1987). However, evidence for the local gregarious populations in spring was frequently based on marginal rainfall and not supported by survey data.

There is evidence from more recent outbreaks that migration from the southern or eastern parts of the species range is involved in the build-up of early summer populations in western Qld. A study of distribution changes from 1995 to 2001, to which the application of wind-trajectory model and insect-monitoring radar technologies, provided a more detailed picture of migratory activity than was previously possible, showed that northward migrations from fledged spring populations in agricultural areas into arid western Qld had occurred on several occasions (Deveson *et al.* 2005).

Northward migrations from swarm populations in NSW in November and early December 1999, contributed to the summer generation in the Windorah area of southwestern Qld, which, after fledging, migrated to the south and west in February 2000. A further successful generation of breeding led to the plague conditions of autumn and spring 2000. There is evidence that similar northward migrations also occurred in 1995, 1997 and 2000, but the resulting gregarious summer generations did not result in large autumn migrations and further population increase. Those findings prompted this re-examination of the likely frequency of migrations to the north or west from agricultural areas, using historical distribution, locust bulletin reports and upper-wind data. Applying the conditions that accompanied these documented recent northward migrations — gregarious fledging populations in peripheral areas during October-November, with only scattered locusts in western Qld, favorable winds and a sudden appearance of swarms in Southwest Qld in November-December — a number of potential northward migrations are identified. The evidence for migrations to Qld from geographically peripheral populations for each year from 1977 to 2002 is summarised. Previous interpretations of the development of several plagues are also re-examined in the light of this evidence.

Methods

The historical analysis of locust migration events depends on indirect evidence. Distribution data from field surveys were used to indicate likely source and destination populations. Identifying immigration usually requires detection of a rapid increase in adult population in an area where a sparse population was previously recorded. The ancillary information we use to support inferred migration events includes the timing of fledging at potential sources, APLC light trap data, radar information, weather patterns, rainfall events and upper-level wind data.

The analysis presented here attempts to identify possible migrations into arid western Qld from gregarious populations of a spring generation from outside that area. The focus on this region was to assess if previous conclusions about its significance are justified. The conditions which would indicate migration to western Qld in November-December from gregarious populations elsewhere were:

- any pre-existing population in western Qld being at low density,
- the existence of gregarious fledging populations in agricultural or peripheral areas,
- the abrupt appearance of swarms in arid Qld,
- the direction of 300-900-m altitude winds in the period prior to swarm appearance,
- reports of emigration from or decline in potential source populations.

Monthly APLC Locust Bulletins and survey records from 1977 to 1995 were examined for evidence of migrations into the Qld arid zone. Bulletin texts often included reports of emigration or a decline in fledged potential source populations and also provided summaries of rainfall and vegetation condition. After 1978, surveys into inland areas were regular and often intensive in Southwest Qld, and therefore give an opportunity to test hypotheses about early generation breeding and outbreak development. The evidence used to derive the early generation sequence leading to historical plagues in 1954, 1972, 1978 and 1984 is also re-examined in the light of possible northward migrations. The available distribution information before 1977 included locust surveys by CSIRO, NSW Agriculture and data collated by Wright (1983).

Distribution data included georeferenced survey records of locust density and development stage taken from road-based ground transects and records of control of high-density locusts. Survey data have been collected by APLC staff since 1977 as part of a rapid-index monitoring program, designed primarily to locate gregarious populations. The occurrence of high-density locusts usually initiates more intensive search. For most years these data provide several samples of the regional habitat areas in each generation, but are largely restricted to the mapped regions in Fig. 2.

A highly clumped spatial distribution is characteristic of gregarious populations, defined here by a density > 2000/ha for adults and > 50/m^2 for nymphs. A 'band' is the term applied to highly aggregated gregarious nymphs with density 100 to >5000/m^2, while density in adult swarms is >50,000/ha. Below these densities nymphal populations are termed 'isolated' (0 to 5/m^2) or 'scattered' (5 to 50/m^2), while adults are termed 'isolated' (0 to 200/ha) or 'scattered' (200 to 2000/ha). Population increase, yielding numerous bands or swarms as a result of at least one generation of breeding, is termed an outbreak.

Maps of the distribution of the spring and summer generations for each season were generated from georeferenced records, but distributions prior to 1986 were digitised from Bulletin maps. Monthly data were combined for September-November and December-January to show the spatial extent of the spring and first-summer generation populations and the areas sampled. If swarms appeared in November in areas where there were previously few nymphs, these were included in the summer distribution. All data points were gridded to 0.5 degree cells and reclassified to the highest of 3 broad density classes for nymphs or adults occurring in each cell. Where gregarious densities occur, a large proportion of the regional population is locally concentrated, so the highest density was taken to indicate the population level in each cell. At very low densities it is difficult to determine where the species is absent, since nil and isolated counts frequently co-occur within a region. The maps provide a graphical demonstration of the frequent seasonal shift in the distribution of gregarious populations.

Where 4 or more of those conditions were met, spring migration into Southwest Qld was assigned and this information, along with the presence of gregarious populations in the different regions in spring or summer, was compared with the similarly identified or documented southward autumn migrations (Table 1). Less stringent criteria were applied to southward autumn migration events to NSW, in that the persistence of gregarious summer populations there did not discount a southward event. The sample size was not large enough to examine the associations statistically.

The predominant trend of upper-level winds throughout the October-April period is from the east and south (Symmons 1986; Deveson *et al.* 2005). Over the 7 years from 1995-2002, upper-level wind direction was between 90°-210° on 50 to 70% of nights with >20°C dusk temperatures at several locations throughout inland eastern Australia. This pattern is maintained for nights with higher velocity winds (>5 m/s and >10m/s), those that have the potential for 9-h displacement of 150 to 500 km (Deveson *et al.* 2005). This trend, and the high frequency of dusk ground temperatures >20°C during November and December, means there will be numerous opportunities for migration to take locusts into western Qld in every year. Intense southward migrations are often associated with cold fronts or troughs. Northward movements also occur on the west side of troughs, but need not be restricted to these conditions. To ensure that winds in previous years, where interpretations of migration dynamics are re-examined, did not differ from this pattern, daily historical upper-wind data (850 to 980 hPa) closest to sunset (1900h or 2000h AEST) and the corresponding ground temperatures for selected years, were obtained from the Bureau of Meteorology

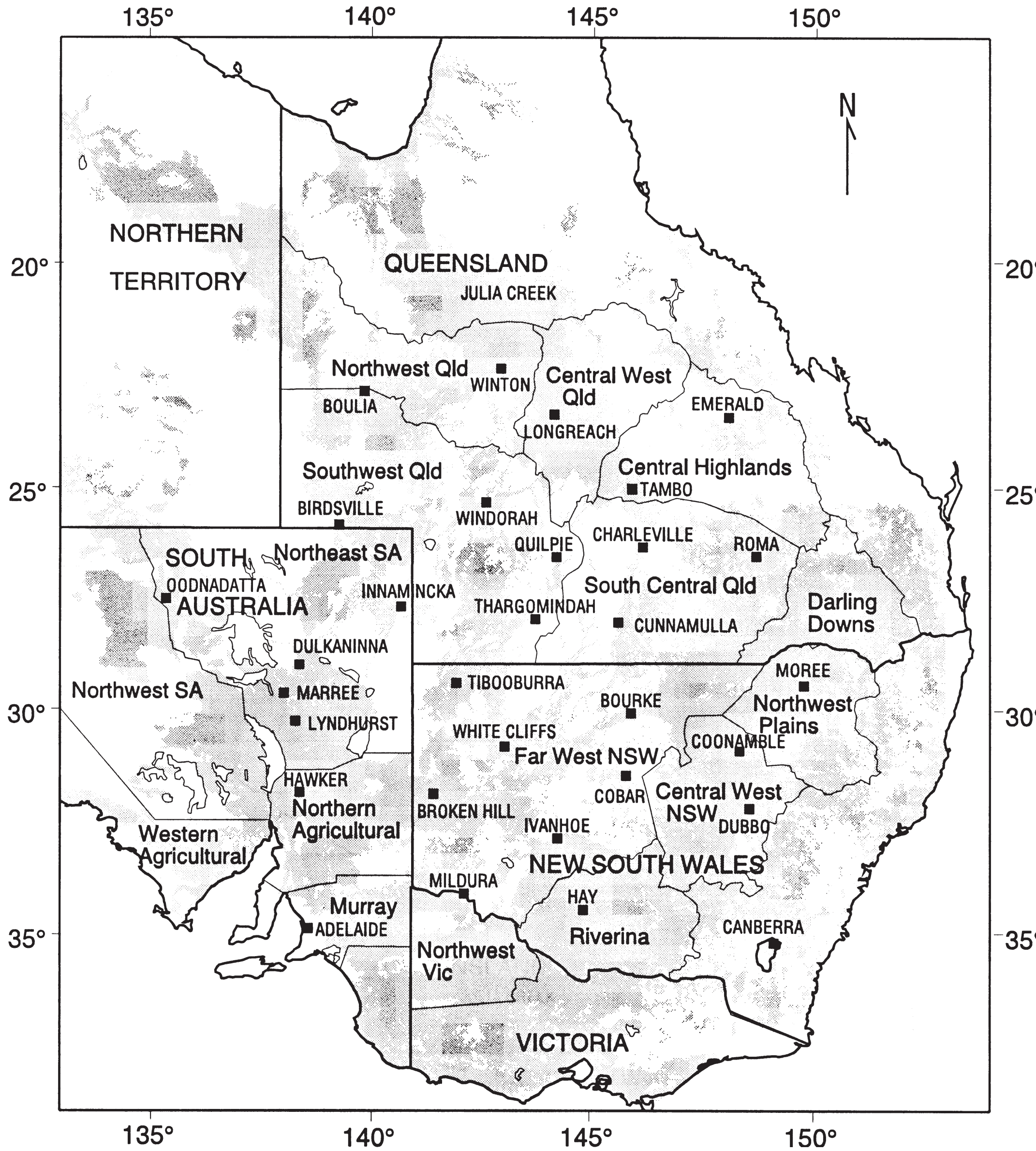

Fig. 2. General regions and locations within the APLC area of operations.

(BoM) and are summarised in Table 2.

Areas described as arid follow the current BoM classification of broad climates (BoM 2003), which uses the 350 mm median annual rainfall as the upper boundary. The term 'agricultural zone' is used here to include noncoastal areas of cropping, areas of non-native pasture, or where trees have been cleared for pasture or grazing, although there is overlap of cereal cropping with the arid zone in the south. All potential habitats are only temporarily favorable and populations drop to nil or isolated (~1/ha) during extreme dry periods. The regions and locations referred to in the text are shown in Fig. 2. These regions are amalgamations of inland rainfall forecasting districts used by BoM.

Results

The likely frequency of late spring-early summer migrations was identified, assuming that the coincidence of a majority of the conditions listed as indicators are sufficient evidence of these events. The many accepted documented southward migrations (Symmons & McCulloch 1980, Bryceson & Wright 1986, Wright 1987) were supported by no more evidence than this, except for some light trap data that were used by Farrow in the analysis of migrations in 1973 (Farrow 1977). Data from early radar studies support migrations to the north in 1974 (Reid *et al*. 1979), 1979 (Drake & Farrow 1983) and1984 (Drake unpub.).

Evidence of northward or westward migrations, from NSW, SA or eastern Qld, into arid western Qld, was found for 1978, 1979, 1984, 1987, 1991, 1992 and 1993. Such migrations may also have contributed to summer populations in 1977, 1980 and 1989. Migration to the west from the Qld Darling Downs, established a swarm population in Southwest Qld in February 1990 and also possibly from Central West Qld in October-November 1989 and 1991. For the years when migration to Southwest Qld is suggested, maps of recorded locust distribution for the spring and early sum-

Table 1. Summary of populations and likely migrations by direction and season 1977-2002. Presence of gregarious populations in spring and summer either in Southwest Qld or the surrounding semi-arid and agricultural margins of NSW, SA or Qld and potential migrations into these areas. Source APLC survey and control data, APLC Locust Bulletins, BoM wind and rainfall data and for 1995-2001, Deveson *et al.* (2005).

	spring generation		summer generation		long-distance migrations	
LOCUST YEAR	southern or eastern margins	Southwest Queensland	southern or eastern margins	Southwest Queensland	potential spring migration to western Qld	potential autumn migration to NSW or SA
1977-78	x		x	x	x	
1978-79	x		x	x	x	x
1979-80	x		x	x	x	x
1980-81	x			x		x
1981-82	x	x	x			
1982-83	x					
1983-84		x	x	x		x
1984-85	x			x	x	x
1985-86			x	x		x
1986-87	x	x	x	x		x
1987-88	x		x	x	x	x
1988-89	x	x	x			
1989-90	x	x	x	x	x [1]	
1990-91	x		x	x	x [2]	
1991-92	x		x	x	x	x
1992-93	x		x		x	
1993-94	x		x	x	x	
1994-95	x		x	x		
1995-96	x		x	x	x	x
1996-97	x	x	x	x		x
1997-98	x			x	x	
1998-99						
1999-00	x		x	x	x	x
2000-01	x			x	x	x
2001-02	x			x	x	
frequency	22	6	18	20	13	13

[1] Possible migration to Southwest Qld in October 1989.

[2] Migration to southwest Qld in late January-February 1991.

mer generations are presented in Figs 3-5.

The evidence for long-distance migrations is summarised in Table 1, although numerous other smaller movements, either within western Qld or agricultural areas, have also been documented. Table 1 summarises the spring and summer population level in Southwest Qld and in surrounding regions, and provides a comparison of assigned migrations in both spring and autumn. This may be a conservative estimate of migratory exchanges because possible migrations into areas where offspring survival was low because of subsequent dry conditions, such as 1980 and 1982, are not counted. Similarly, the presence of already gregarious-level populations in Southwest Qld in spring, such as 1981 or 1986, obscures any supplement to the population from immigration.

In 13 seasons, most of the conditions indicating northward or westward locust migrations into Southwest Qld in late spring and early summer were met. South or southeast winds above the 20°C temperature threshold were a dominant feature of the general weather circulation during these times (Table 2) (Deveson *et al.* 2005). During spring, gregarious locusts were common in the southern (NSW and SA) or eastern (South Central Qld, Darling Downs, Qld Central Highlands) part of the species-range in eastern Australia, but occurred far less frequently in western Qld. In the 25 seasons included (1977-78 to 2001-02), nymphal bands and swarms of young adults were present during October-November in NSW or SA in 22 y, but only in 6 y in Southwest Qld (Table 1). However, by late November or December, usually after rain, swarms were found in western Qld in 20 seasons, as often as in NSW.

In 2 years, 1983 and 1986, gregarious spring populations in southwest Qld did contribute to large summer populations in this region, from which migrations to agricultural areas occurred in autumn. In 1983-84 migrations from western Qld in late summer established the large plague infestation in autumn 1984 and the following spring, while in 1986 to 87, similar migrations appear to have supplemented an already large population in NSW.

Table 2. Predominant wind directions during November and December for selected locations and years of interest. Evening wind (980 to 850 hPa) direction classified by compass-sector heading. Nights where data were missing or where the wind direction was variable are indicated in the right hand column. Numbers in brackets indicate nights where the evening temperature was below the 20°C take-off threshold for Australian plague-locust flight. For the 1950s, only Charleville and Mildura were recorded, with Moree, Cobar and Longreach added by the 1970s.

		Number of nights during November and December where predominant wind direction was in compass sector				
Year	Location	North	South	East	West	Missing or variable
1954	Mildura	29(4)	5	15	8	4
	Charleville	33	8	3	14	3
	Cobar	–[1]	–	–	–	–
	Moree	–	–	–	–	–
1972	Mildura	38(3)	1	11	7	2
	Charleville	26	9	14	11	1
	Cobar	31	2	14	12	2
	Moree	21	13(1)	5	17(1)	5
1978	Mildura	34(5)	7	13(1)	7	0
	Charleville	37	6	4	11	3
	Cobar	32	8	10	11	0
	Moree	18	13	16	14(2)	0
1984	Mildura	28(3)	4	17	8	2
	Charleville	34	4	1	14	8
	Cobar	33	6	11(1)	6	5
	Moree	26	7	10	8	10
1987	Mildura	25	5	7	5	18
	Charleville	28	7	4	18	12
	Cobar	25	10	12	11	1
	Moree	15	13(1)	10(1)	18	5
1991	Mildura	14(1)	4	15(2)	6	17
	Charleville	32	6	9	12	2
	Cobar	29	8	15	6	3
	Moree	19	11	12	9	9

[1] no data available

The early breeding sequences leading to several of the historical plagues examined by Wright (1987) — 1955, 1973-74, 1978-79, 1983-84 — are re-examined below. In some years the immigration of spring-generation adults from outside western Qld would appear to be an alternative source for gregarious summer populations in that region. Summaries of the location and sequence of breeding events, and the likely direction of major long-distance migrations between generations, in each season from 1977–1994, are given in Appendix 1. They include any reference to fledging, reported population decline or migrations from gregarious spring populations, or the relatively abrupt appearance of swarms in southwest Qld.

Re-interpretation of historical plagues

1953-55.—Information available for the season prior to the autumn 1953 invasion of swarms into agricultural areas in NSW, SA & Vic is inadequate for drawing conclusions about prior generations. There were reports of locusts from the Northwest Plains and Far west NSW in spring 1952, but the population was not widespread (Magor 1970). There was general agreement that swarms migrated from Southwest Qld and adjacent Far Western NSW in late summer 1953 (CSIRO 1954). Concluding there were 2 separate plagues in 1953 and 1955, derived independently from breeding in the arid inland (Wright 1987), is less certain, since it was drawn from the dry conditions and decline of populations in the agricultural areas in summer 1954-55. However, swarms were widespread from the NSW Northwest Plains to the eastern Riverina in November and December 1954, and persisted in the north until January 1955. The limited upper-level winds dataavailable for the time (Table 2), suggest that migration from these areas may have supplemented the summer generation in inland Qld in 1954-55.

1973-74.—The development of the 1973 plague has been studied several times and its progress from the summer generation in Far West NSW, southwest Qld and Central West NSW is well documented (Farrow 1977, 1979, 1982a, 1982b). However, the source of the swarms first reported between Charleville and Quilpie in South Central Qld at the end of November 1972, which, along with swarms from Central West NSW, gave rise to 2 more generations before the autumn invasion of the southern NSW agricultural zone in late March 1973, appears only to have been identified from rainfall records. Both NSW and Qld were infested in the previous seasons and CSIRO conducted surveys in Qld from 1970, but the program ceased in May 1972. A survey of South Central Qld the following spring found no evidence of a spring generation and the first reports of locusts in Qld were of immigrant swarms around Quilpie in late November 1972.

Clark (Anon. 1974) concluded that the only area with sufficient spring rain to provide a source for these immigrants was a small area south of Longreach on the Barcoo River. Clark identified disturbed weather on the east of a trough on 28 November 1972 as the migratory event. This was the only night with northerly winds that could have brought locusts from Longreach, but this was several days after the first reports of swarm arrival on November 24 (CSIRO unpub. reports). Upper-level winds at Longreach and Charleville were predominantly from the south and east from November 11 to 27 (Table 2).

Wright (1983, 1987) identified a very broad area of western Qld as having suitable rainfall for the spring 1972 generation. In either case, however, the fledging time would have been midSeptember (Wright 1987), leaving adults to persist in dry conditions for 2 mo before appearing around Quilpie.

Alternatively, the large fledging population across the NSW Northwest Plains and Central West, extending into the Qld Darling Downs in November 1972 is a potential source for the swarms reported in Qld during November. Migratory activity from these developing swarms was reported, followed by a decline in numbers in NSW by December.

1978-79.—The early development of the 1979 plague could be reinterpreted within the framework of exchange migration. Extensive APLC surveys throughout the arid inland in October 1978 detected only sparse nymphs, and only scattered adults were found in western Qld in November and December 1978. At the same time there was a widespread gregarious population in the Central West of NSW, with bands around Coonamble and in the eastern Riverina, fledging during November. In late November laying swarms moved west towards Bourke from the Central West and laying was also detected in the northwest corner of Far West NSW and in adjacent Southwest Qld. The likely adult immigration extended into southwest Qld and Northeast SA, where rains >40mm fell in late November.

Despite more surveys in December, no further gregarious populations were detected in western Qld. But in late January 1979 large numbers of gravid swarms were found throughout Far West NSW and the adjacent corners of Southwest Qld and northeast SA, and swarms were also still present in the western Riverina. Heavy rainfalls in the inland in late January and February 1979 ensured high recruitment in the offspring generation of those swarms, which led to large numbers of bands in February. The available wind data for November 1978 show frequent winds from the south and east throughout the month (Table 2), and the Roma (Qld) light trap also recorded high numbers of *C. terminifera* on November 25 and 26, so migration from NSW to the west and northwest during November 1978 could explain the appearance of gregarious adults in Far West NSW at that time. There was also a local population in Far West NSW in late November 1978, as evidenced by reported late-instar nymphs. After analysis of rainfall in subareas of the arid inland, Symmons & Wright (1981) concluded that the area north and west of Longreach was the most likely source, because the rainfall sequence in other areas was insufficient to allow for spring population increase. The available survey data show no evidence for this (Fig. 3c).

1983-84.—The March-December 1984 infestation gives the best evidence for a plague drawn solely from sequential generations within the arid inland. In contrast to other plagues there were no known gregarious populations in other areas in eastern Australia in the months preceding the outbreak. A gregarious spring generation was detected as 'fledging concentrations and some swarm density adults' (APLC 1984) in Southwest Qld (27°S) in October 1983 and another population detected in the Qld Central Highlands. Emigration from Southwest Qld in early November was shown to have initiated a summer generation, first detected as laying swarms in the Longreach area in late November. Further emigrations from the same area on 13 to 14 November to the east, were taken to have generated a large population in the Thargomindah area, subsequently identified as the source of the plague (Bryceson & Wright 1986), although no population was found. Heavy rains each week in December 1983 created conditions for a huge population increase. By early January 1984, gravid swarm-density adults had spread into the Charleville area of Central West Qld, west to Birdsville in Southwest Qld, and to near Bourke in NSW. Over following weeks gravid adults spread throughout NSW. It is likely that the southerly migrations during January were from widespread Qld populations including Longreach-Blackall, rather than the identified source area. Successful breeding of this generation led to the plague conditions the following spring.

Discussion

Distribution data show that the appearance of swarms in early summer in Southwest and Northwest Qld occurs much more frequently than there is any local gregarious spring population. Eggs laid immediately after rains or emerging from quiescence could not produce adults within the time that swarms are often observed. Given also that, in the absence of migration, fecundity rates indicate 2 generations are required to develop swarms from sparse populations (Clark 1972, Farrow & Longstaff 1986), then the question is whether aggregation of isolated or scattered-density adults can explain the formation of swarms immediately after rain. The mechanics of such convergent local migration and the area from which locusts would have to be drawn remain arguable, but often there is also a regional increase in population, coincident with the appearance of localised swarms. We conclude therefore that long-distance migration plays a part in the formation of swarms in early summer. High-density populations of recently fledged young adults are frequently found in NSW, SA or further east in Qld in November and December to provide potential sources of large numbers of migrants.

This qualitative analysis of APLC population distribution data after 1977 suggests that mass migration to arid western Qld from already gregarious swarm populations further south or east has occurred on numerous occasions. The number of years that northward migrations from spring generations were likely, is comparable to that of the better-known southward movements of late summer and autumn (Table 2). This supports the hypothesis established from studies of recent population movements that there is frequent exchange migration of *C. terminifera* across a much wider geographic arena (Drake *et al.* 1995) than was previously appreciated (Wright 1987). The typical early season distribution is one of gregarious populations in the southern and eastern part of the distribution area, where winter rain is common, fledging during October and November. On few occasions over the last 25 y have any gregarious populations been found in Southwest Qld during spring, and except for 1983 and 1986, these fledged by October and declined before the arrival of summer rains. In those 2 y, however, the local spring populations did lead to the development of large infestations in the autumn. In other seasons, such as 1988 and 1990, a suitable sequence of winter and spring rains in southwest Qld did not produce a gregarious spring population.

Reasonable evidence exists for migrations from NSW or SA into arid western Qld in half of the last 25 y, while migration from further east in Qld has also contributed to summer populations on several occasions. The frequency of such migrations appears to be equivalent to that of the better known southward migrations from that region in late summer and autumn, although they may be more diffuse and their impact less dramatic. Northward movements within NSW, within western Qld, or from the Northwest Plains to adjacent areas of Qld, were detected at the time in 1979, 1987, 1991 and 1993 (APLC 1980, 1993, 1994; Hamilton *et al.* 1993), but swarm development in Southwest Qld was always attributed to aggregation of a widespread scattered population, undetected gregarious breeding, or movement from elsewhere within Western Qld.

The predominant direction of upper-level winds over southeastern Australia at night is to the north and northwest, with nights of southerly wind trend occurring at twice the frequency of other directions in some years. While dusk temperature for many of these nights in spring is 20 to 25°C (Symmons 1986), which may reduce migrations, there remain ample opportunities for significant movements to the north and northwest.

This interpretation of migrations is based on indirect evidence and remains open to challenge. Identifying the relative contributions of local and long-distance immigrants to the swarms of the first summer generation in western Qld is often difficult to determine. The migration process affects regional populations and may have the effect of widespread dispersal or convergence (Clark 1971). Over a sequence of nights migrations from the same region may occur in several different directions, as is likely to have occurred in 1979-80, 1984-85 and 1993–94 (APLC unpub.), and migrants may

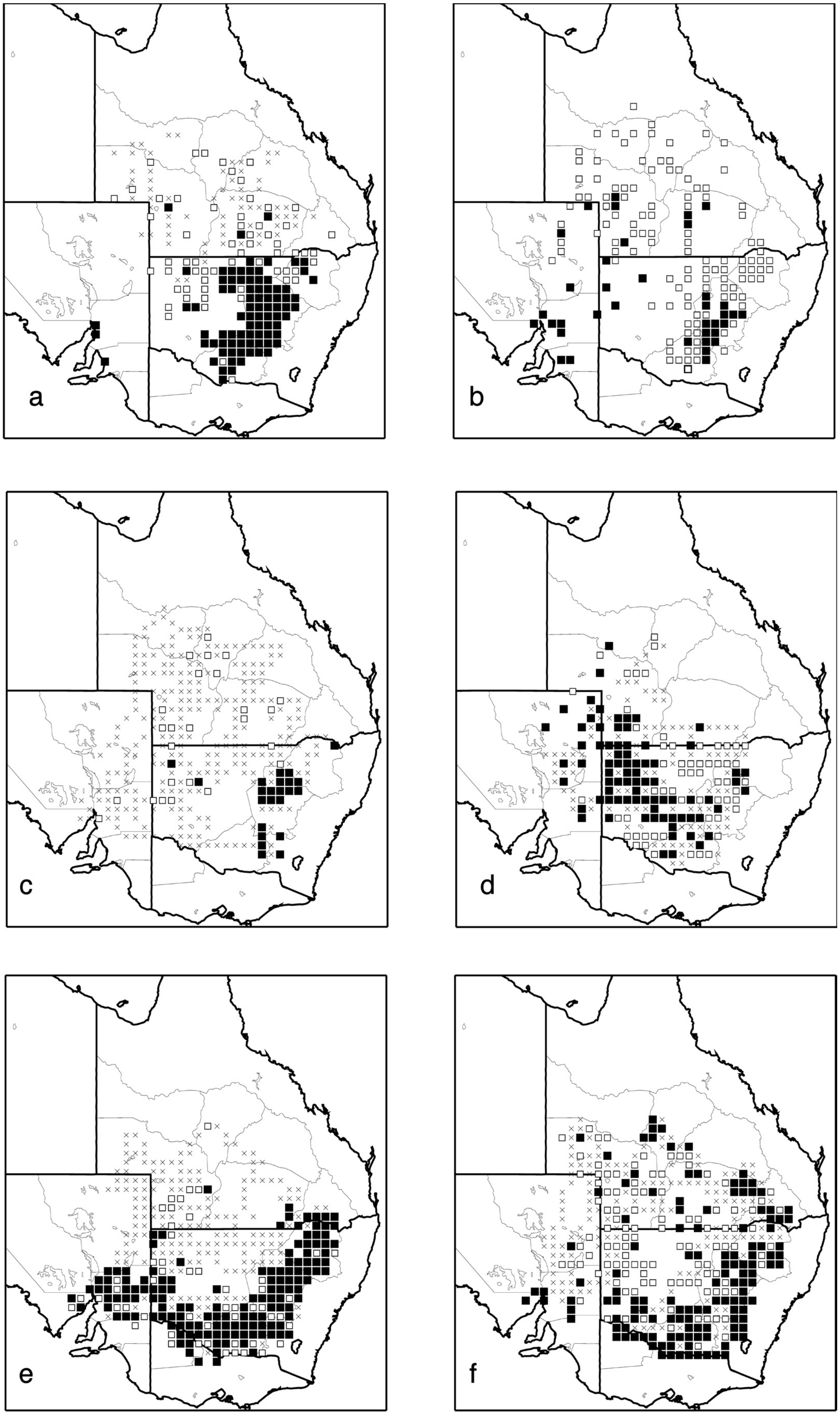

Fig. 3. Distribution of spring (October-November) and summer (December-January) generations of *C. terminifera* before and after migrations in late November and early December for 1977-1978 a) spring, b) summer, for 1978-1979 c) spring, d) summer and for 1979-1980 e) spring, f) summer. Symbols are generated from APLC survey and control data using the highest density count for each 0.5 degree cell. × – nil-isolated, □ – scattered, ■ – gregarious adults or nymphs.

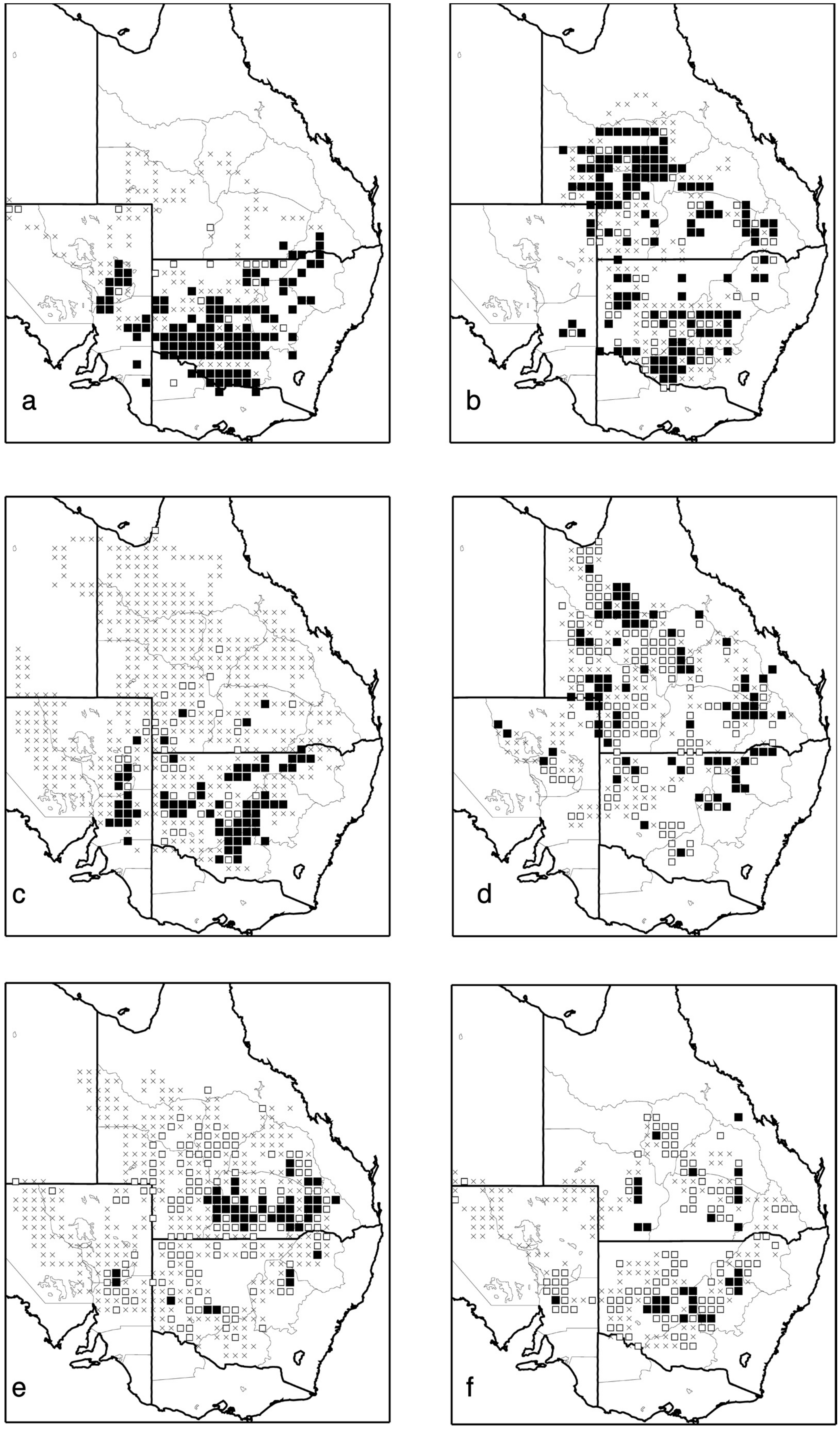

Fig. 4. Distribution of spring (October-November) and summer (December-January) generations of *C. terminifera* before and after migrations in late November and early December for 1984-85 a) spring, b) summer, for 1987-1988 c) spring, d) summer and for 1990-1991 e) spring, f) summer. Symbols are generated from APLC survey and control data using the highest density count for each 0.5 degree cell. × – nil-isolated, □ – scattered, ■ – gregarious adults or nymphs.

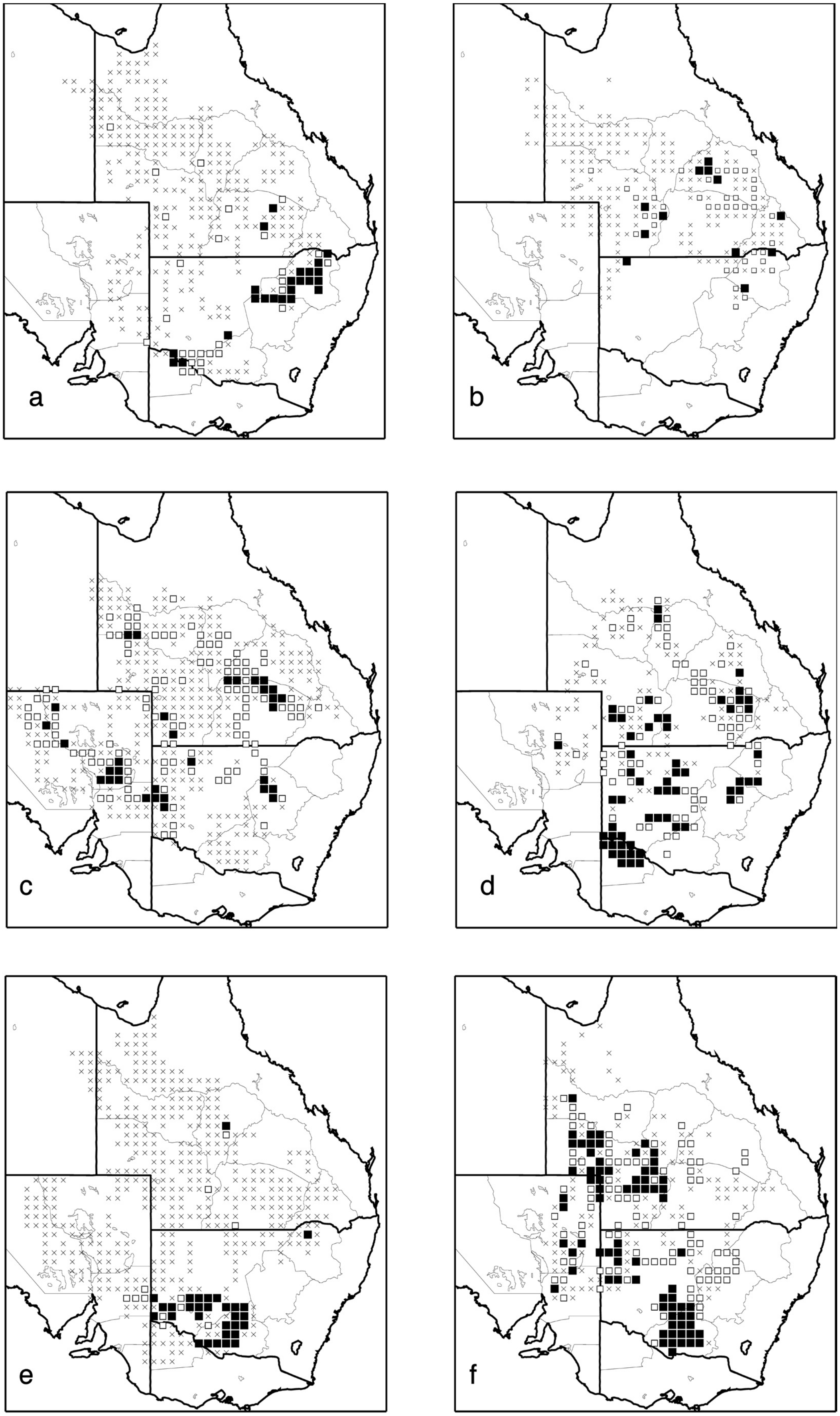

Fig. 5. Distribution of spring (October-November) and summer (December-January) generations of *C. terminifera* before and after migrations in late November and early December for 1991-1992 a) spring, b) summer, for 1992-1993 c) spring, d) summer and for 1993-1994 e) spring, f) summer. Symbols are generated from APLC survey and control data using the highest density count for each 0.5 degree cell. × – nil-isolated, □ – scattered, ■ – gregarious adults or nymphs.

move several times.

Most previously documented migrations in NSW were on warm northerly flows ahead of depressions, which led to the conclusions that such southward movements were dominant (Farrow 1977, 1979, 1982b). These observations, the low-level movement of swarms by day, and the pattern of southward late summer and autumn migrations from western Qld occurring ahead of frontal systems, may have led to the proposition that arid southwestern Qld is the 'plague source area' (Symmons 1984) and the identification of spring breeding within that area as critical to plague initiation (Wright 1987). In Wright's analysis 'source' is used to indicate that all prior generations to a plague developed within the same restricted area, rather than just the penultimate generation. This is clear from the invocation of 'spring laying by overwintering adults', and 'spring laying by adults fledged from overwintering eggs' within that region to explain the initial generations in each plague.

Five of the 6 historic infestations identified as plagues by Wright (1987) were preceded by at least one summer generation and by widespread heavy rainfall in the normally arid inland, but they probably did not all originate from a sequence of breeding in the arid region centered on the southwest corner of Qld. Five of those infestations were also preceded by gregarious spring populations of *C. terminifera* elsewhere within its range, which for more recent outbreaks have been shown to have the potential to provide significant immigration into western Qld. Reasonable evidence for a plague originating solely from breeding in Southwest Qld exists only for 1983-84, where the very low populations at the end of the 1982 drought and the sequence of breeding traced in the interior from November 1983, indicate an origin in the arid inland. We argue that the migration of already gregarious fledging populations from other areas of potential habitat in NSW, Qld or SA (Fig. 2) in late spring-summer into western Qld, more frequently contributes to the summer generations in Qld. This is essentially a return to the proposition of Clark and Davies (CSIRO 1972), who, after studying populations in western Qld from 1969-71, suggested a seasonal 'migratory circuit' with movement on prevailing winds into western Qld in early summer, and southward migrations in late summer and autumn ahead of depressions.

The development and persistence of the arid 'plague source area' model may also be attributed in part to the fact that on two occasions in the 1980s, spring breeding within Southwest Qld did clearly contribute to major infestations. That model of migration dynamics for the Australian plague locust provided a useful framework and focus for understanding the frequent pattern of summer and autumn migrations from western Qld leading to pest infestations of agricultural areas, but in its simplification and rejection of remigrations into arid western Qld, it imposed an ecology that is inadequate both in terms of observed population distributions and (possibly) for the evolutionary development of migration in the species (Deveson *et .al* 2005). A more complex pattern of regular exchange migration between regions of temporarily favorable habitat is now indicated. The success of these redistributions depends in part on the seasonal distribution and the actual sequence of rainfall. In a classic early text on insect migration, Williams (1958) pointed out that return migrations were often less dramatic and less visible than well-known migrations in one direction, and further suggested that where return movements were unknown, it was more a reflection of our level of ignorance than our knowledge about true migratory species. It would appear that migration in *C. terminifera*, which produces successful population interchange between generations throughout the large area of potential habitats in inland Australia, is no exception.

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Appendix 1

Summaries of annual dynamics

1977-78: Limited locust distribution data from western Queensland in early spring makes it difficult to identify the source of populations that developed in this region in summer. However, given the timing of distribution changes, northward migrations may have contributed. In spring 1977, bands were present in the NSW Northwest Plains and Central West and Riverina and extended into the southern part of Far West NSW, while only a scattered adult population was found throughout Qld (Fig. 3a). Fledging of the NSW population occurred in November 1977. In early December, adult numbers increased to gregarious density in South Central Qld, Southwest Qld and adjacent parts of NSW and SA (Fig. 3b). Predominant wind directions (Table 2) were from the south at this time.

1978-79: See re-interpretation of historical plagues.

1979-80: Spring 1979 began with a large infestation across the agricultural zone of NSW and extending into the Darling Downs of Qld and Northern Agricultural SA (Fig. 3e). This was the height of the 1979 plague (Symmons & Wright 1982). At this time there was only a scattered population in Southwest Qld and the north of Far West NSW, but gregarious adults appeared in these areas during November after fledging in the agricultural areas. Swarms appeared in South Central Qld near Roma, identified in the APLC Locust Bulletin as migrating from the south on November 17, and were also subsequently found as far north as Longreach. Gregarious adults appeared in Far West NSW, north of Broken Hill, and from Bourke north into Qld (Fig. 3f). The rapid distribution change suggests northward migrations from the large fledged population in NSW, and this is supported by radar observations in Central West NSW (Drake and Farrow 1983). There were moderate rains in Far West NSW and Southwest Qld in December, and adult numbers increased. A second generation of gregarious adults developed in Central West and South Central Qld from Longreach to Roma and in the Northwest Plains of NSW during January. Southward migration from the Longreach area brought swarms into Southwest Qld and, along with migration from within NSW, contributed to the appearance of swarms around Bourke and in Central West NSW in February. These locusts then laid overwintering eggs that hatched in the spring of 1980.

1980-81: Spring 1980 began with small gregarious hatchings in Central West NSW and the eastern Riverina and near Tibooburra in Far West NSW. Despite an intensive survey in Southwest Qld, only isolated adult locusts were located and conditions were dry. Fledging of the populations in Central West NSW occurred in early November and emigrations were reported from 5-14 November, but migrants to Qld would have encountered dry conditions. There was a single large catch at the Roma light trap on November 28. By January only a scattered population remained in the Riverina and near Roma in South Central Qld. Numbers increased in February with widespread isolated hatchings and by March a gregarious population had developed in Southwest Qld. There was some migration from here in late March south into Far West NSW.

1981-82: There was widespread winter rain in April and May 1981 and by late August there was a fledging gregarious population in Southwest Qld, but this declined to scattered density by October 1981. Bands developed in Far West NSW from Tibooburra to White Cliffs and in the Northwest Plains, and in South Central Qld north of Roma, the Qld Central Highlands and the Darling Downs in October. In December 1981, a second generation of nymphs developed near Roma and in the Central West and Northwest Plains of NSW, which fledged in January 1982 and the resulting swarms spread into Central West NSW. A third local nymphal generation produced some swarms in March 1982 that migrated into the Riverina in NSW.

1982-83: The NSW Central West and Riverina produced a gregarious spring population, while only isolated locusts were found in inland areas because of drought conditions. The NSW population fledged in November with some emigrations reported, but the population declined in drought conditions. Scattered-density adults were found in Qld during December and January 1983. In February 1983, a gregarious population of fledging nymphs was found near Oodnadatta in Northwest SA, but the population declined in March. The season finished with very low locust numbers, but sparse nymphs were found in Southwest Qld in April, either from immigrants or local breeding.

1983-1984: See re-interpretation of historical plagues.

1984-85: In the spring of 1984, a large infestation developed in NSW and control was carried out over 280,000 ha. Bands in the Riverina of NSW fledged in November and migration of swarms from here into the Central West and Northwest Plains of NSW and into southern Qld was documented, along with a drop in population at infestation areas such as Ivanhoe. Few locusts were found in western Qld during surveys in September and November (Fig. 4a), but swarms were then reported from the Longreach area in Central West Qld during December 1984, along with isolated swarm reports from Tambo to Winton in Northwest Qld associated with heavy rain. Radar observations in the Riverina (A. Drake unpub.) detected several northward migrations, as well as a large southward movement during November and December. By January there was a widespread gregarious population in Qld. Upper-level winds during December show repeated opportunities for migration to the northwest. A dry autumn in all areas in 1985 led to a population collapse.

1985-86: Surveys in September 1985 detected no populations in Qld, despite good autumn and winter rainfall in the inland. There was rain in October and widespread heavy rain in early November, but intensive surveys during November and December 1985 again found only isolated locusts in Qld and NSW. By January 1986 adult populations in the NSW Central West and south of Longreach in Central West Qld reached gregarious density. The latter produced bands that developed into swarms during March 1986, which probably migrated into Southwest Qld.

1986-87: Following winter rains in 1986, an area of bands and fledging swarms was located in Southwest Qld in October 1986. These locustswere monitored and emigrations reported from October 18. Bands of late instar nymphs were found in the Central West of NSW in November. Gregarious adult populations and fledging nymphs were also found in the Riverina, and in Far West NSW from White Cliffs and Bourke in late November. The presence of nymphs in these NSW populations make it unclear if these included migrants from Qld (APLC 1988). There was rain in NSW in November and in Qld in December. In mid-December 1986, swarms were found in the Longreach-Windorah area, probably derived from the persisting local population in Southwest Qld. By February 1987 a widespread population in Qld extended south to Thargomindah and to Charleville in South Central Qld. In NSW swarms were found from Bourke to the Northwest plains, the Central West and the Riverina, the result of migrations from the north and resident populations.

1987-88: In spring 1987 infestations of bands occurred right across the agricultural areas from the Northern Agricultural (SA) to Bourke in western NSW (Fig. 4c). Control began in September 1987 around Bourke and Broken Hill and 100,000 ha had been controlled by the start of fledging in late October. Few locusts were seen on spring surveys in western Qld, but some bands developed north of Cunnamulla in South Central Qld. Migrations were observed in late November from the Bourke area to the Northwest Plains around Moree and by mid-December locust numbers had dropped in the spring-control areas (Fig. 4d). Large numbers of *C. terminifera* appeared in the Longreach light trap from November 21-30, coincident with the appearance of swarms in the Winton area of Northwest Qld. While these swarms may have come from undetected breeding and migration from central Qld (APLC 1989), upper-level wind data for November 1987 support possible northward migration from NSW (Table 2). Further migrations to the west, associated with rains in late December 1987, established a cohort in Northeast SA and Southwest Qld. By February 1988 a gregarious swarm population had developed in SA near Oodnadatta, from which there were migrations to the west or south during March.

1988-89: There was good winter rainfall in the arid zone in 1988 and spring surveys found a widespread scattered adult population and evidence of movements as early as August, but very few nymphs outside of Northwest SA. A dry spring led to a decline in numbers in all regions except for a localised scattered population of adults and sparse nymphs in Southwest Qld. Despite widespread rain and extensive surveys in summer-only scattered locusts were found in Qld. A gregarious population with some swarms developed in Central West NSW by February 1989.

1989-90: There were widespread rains in May and June 1989 and by September there was already a scattered adult population in Northeast SA and north of Broken Hill in Far West NSW. By early October fledging bands and swarms were found in South Central Qld near Roma and a widespread population in Northeast SA and Far West NSW reached gregarious level, while bands also developed in Central West NSW. Heavy rains fell in late October 1989 in Qld and NSW and in early November swarms were found near Windorah in Southwest Qld. Populations increased substantially in Southwest and Northwest Qld during December 1989 and January 1990, while in NSW swarms developed in the Central West and moved into the Riverina. Populations decreased in all inland areas from February 1990 as a result of dry conditions and emigration, while some swarms persisted in the Riverina in NSW and in South Central Qld.

1990-91: Widespread autumn and winter rains occurred in western Qld, and in August 1990 scattered adults and sparse nymphs were found there. In September bands developed in South Central Qld which, following fledging in October, migrated northeast to the Central Highlands and east to the Darling Downs (APLC 1992), where eggs were laid on further patchy rains (Fig. 4e). At the same time a low-level population in NSW was fledging. Surveys in December 1990 and January 1991 still indicated a low population in Southwest Qld, but there were heavy rains in January and early February. Migrations occurred with the February rains, into Southwest Qld from the infested areas further east in Qld. Upper-level winds for the month of February 1991, as well a decline in population in the Darling Downs and Central Highlands, and light-trap data from Birdsville and Longreach, also support this movement. Eggs laid by the immigrants in Southwest Qld gave rise to gregarious nymphs, followed by swarm populations in March 1991. The population in Central West NSW also developed swarms during March. Significant autumn laying was recorded from the Northwest Plains of NSW, South Central Qld and part of Southwest Qld.

1991-92: Winter rainfall in 1991 was restricted to NSW and eastern regions of Qld. Surveys in September and October 1991 found bands near Roma in South Central Qld and in the Northwest Plains and Central West of NSW, but few locusts in western Qld. There was also an infestation in the south of Far Western NSW and Northwest Victoria (Fig. 5a). The bands in Qld fledged through October 1991 but numbers declined in dry conditions. In NSW band infestations developed around, Coonamble and Narrabri in the Central West during October, with swarms appearing late in the month. There were also many reports of adult locusts in Far West NSW at that time. The population declined in NSW during November 1991. Swarms appeared suddenly in Southwest Qld near Thargomindah from November 22 and continued to move north as far as Longreach. Upper-level winds for the period prior to their appearance indicate that migration from the large fledged population in NSW at that time is a likely source of those swarms. The population in the Mitchell-Roma area in South Central Qld, which fledged in October and subsequently declined, may also have contributed. Bands followed in western Qld in December 1991 and by January 1992 there were swarms in the Southwest, Central West and Darling Downs of Qld (Fig. 5b). A further nymphal generation occurred in Southwest Qld during February, and in early April 1992 southward migrations took locusts from Qld into northern SA and Far West NSW. The populations present in the Northwest Plains of NSW bred successfully during spring and summer 1991-92, migrating to the eastern Riverina in the autumn of 1992.

1992-93: There was winter rainfall in NSW and northern SA in 1992. Spring infestations occurred in the Northwest, Northeast and Northern Agricultural districts of SA, extending east to Broken Hill in Far West NSW. There were widespread rains in September 1992, but extensive surveys in September and October in Southwest Qld found only sparse nymphs and scattered adults, with numerous-density nymphs in Northwest Qld, while nymphs up to band density and fledging adults were found in South Central Qld around Roma. Bands also formed in the NSW Central West in October 1992 (Fig. 5c). Fledging in northern SA began in mid-October and from early November swarms appeared in Far Western NSW and in Southwest Qld. Migration from SA probably contributed to these populations, but upper-air data are unavailable. There was widespread heavy rain on several occasions during the month. Bands of the subsequent generation developed in January 1993 in Southwest Qld and Far West NSW, with swarms in February. The infestation in Far Western NSW was widespread and continued rains led to population increase at each generation (Fig. 5d). Over 3 generations to the end of April 1993 > 300,000 ha of control was carried out in NSW. In NSW autumn laying occurred in the southern part of the Far West, Riverina and Northwest Plains.

1993-94: Rains were widespread in May and July 1993 throughout most of the NSW infestation areas. The anticipated spring outbreak began with bands in September and October in the south of Far Western NSW, the Riverina and Northern Agricultural SA. There was a gregarious population in Central West Qld, with bands that fledged in late September. Spring surveys in western Qld detected sparse nymphs and isolated adults (Fig. 5e). There was further rain in early October in NSW and band control began in several areas, with fledging of nymphs through November. Swarm control followed from November 10. About 250,000 ha of aerial control was carried out on bands and swarms. The passage of several trough systems from November 17 – December 5 1993 produced potential migrations in different directions over a sequence of nights. Migrations were inferred from the populations in the Riverina and Far West NSW by arrival of adults in other parts of NSW and the use of an early wind-trajectory model, first to the east on November 18, then to the north on 19-21 November. On November 25-26 strong northerlies took locusts as far south as the Victorian coastline (APLC 1995), but from 28 November to 5 December winds again would have taken locusts north, coinciding with reports of arrivals around Bourke and Thargomindah in Southwest Qld. Swarms were found in Southwest Qld from mid-December 1993 and in the area north of Broken Hill later in the month. The limited survey in these areas in November makes distinguishing sources difficult, but northward migrations are indicated. The following nymphal generation formed some bands in Southwest Qld, Far Western NSW and adjacent SA in January 1994 (Fig. 5f). Heavy rains fell over much of Qld and NSW during February and southward migration to the Bourke area from Qld was documented.

1994-95: Winter rains were restricted to the south and east of the range and spring surveys detected gregarious nymphs in the northern Riverina and the Northwest Plains of NSW and Northern Agricultural SA. In November a nymphal population developed around Roma, South Central Qld, which had remained as quiescent eggs until rain in late October 1994. Southwest and Northwest Qld remained dry until mid-November. In early December 1994 a small area of swarms was found near Marree in Northeast SA, possibly derived by migration from further to the south during November. December 1994 was dry and virtually no locusts were seen in Southwest or Northwest Qld or Far West NSW, despite extensive surveys, until February 1995 after several widespread heavy rains during January. A widespread hatching of isolated nymphs was detected in Southwest Qld, and to a lesser extent in Northeast SA during February and by April 1995, adult numbers had increased to gregarious levels in Southwest Qld and also in Central West NSW.
1995-2002: The event sequence in these years is covered in Deveson *et.al* (2005)