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Adaptations of locusts and grasshoppers to the low and variable rainfall of Australia

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Abstract

In Australia, where approximately 80% of the land area is arid or semiarid, rainfall is the major factor limiting acridid populations. Rainfall is not only limiting in terms of quantity but also in being highly variable, both temporally and spatially. In this paper, the main adaptations seen in Australian Acrididae to overcome limiting rainfall are discussed with special reference to economically important species.

In the arid to semiarid subtropics (lat 23-33°S) rainfall is slightly summer-dominant but extended dry periods can occur in any season. *Chortoicetes terminifera*, the main pest species, avoids dry periods through embryonic diapause or survives dry periods as quiescent eggs or adults. Migration is critical for survival as it allows locusts to locate areas of localized rainfall. Outbreaks are frequent and develop when enough rain falls to allow continuous breeding over three to four generations.

In temperate areas of subcoastal southern Australia, summers are dry and most rain falls in winter or early spring. *Austroicetes cruciata*, a univoltine pest species, avoids the dry summers by having an embryonic diapause between summer and early winter.

In the tropical north (lat 13-23°S), rainfall is strongly summer-dominant and *Austracris guttulosa*, another univoltine species, survives the dry winter as immature adults in reproductive diapause. Adults mature after feeding on the green vegetation present following early rains of the wet season. But the early rains are often localized and adults migrate until they encounter these localized areas of rain. Adults then mature and lay, but the survival of their offspring eggs and very young nymphs is assured only if there is further rain within 6 weeks. Outbreaks develop only when there are several years of regular rains both in outbreak areas and adjacent areas of the arid zone.

Locusta migratoria does not have a stage that can survive extended dry periods. Consequently, it is mainly restricted to subcoastal areas of moderate rainfall. In the main outbreak areas of subtropical Queensland, populations often decline during the commonly dry winters but outbreaks develop when good rain falls in all seasons.

Key words

Acrididae, adaptations, Australia, rain

Introduction

A clear understanding of the mechanisms and ability of locusts and grasshoppers (Acrididae) to overcome limiting factors in their environment is essential for predicting when and where outbreaks are likely to occur. Climate, principally rainfall, is considered to be the main force regulating many insect populations, including those of acridids (Andrewartha & Birch 1954). Lack of rainfall is usually cited as the main factor limiting population increase in acridids inhabiting tropical semiarid and arid areas, while those species occurring in more temperate or marshy areas are favoured by years of subnormal rain. Joern (2000) has questioned the validity of using such simple climatic-driven models to explain fluctuations of North American grasshopper populations. He argues, as other authors have previously (*eg.*, Dempster 1963), that acridid populations are more likely to be regulated by the combined effects of abiotic forces (climate) and biotic interactions (competition, predation, parasitism). Such abiotic and biotic factors have been shown to be important in grasshoppers in subcoastal temperate areas of eastern Australia (Baker 1993), but we argue that in the more than 80% of Australia that is arid or semiarid (Williams 1979), lack of rainfall is the main factor limiting acridid population increase, through its direct effect on food quality and abundance. Furthermore, the adaptations seen in Australian acridids to overcome an environment where rainfall is often limiting, can explain their pest status and help to predict the likelihood of an outbreak.

Major rainfall zones in Australia .— Australia is considered to be the driest inhabited continent in the world. Fig. 1 shows the main climatic zones of Australia based on rainfall (Australian Bureau of Meteorology 2001). The arid zone (median annual rainfall < 350 mm) dominates the land mass and is divided into a mostly summer rainfall area and an area where no distinct seasonal difference occurs. In the tropics, rainfall is strongly summer-dominant and there is a distinct dry winter season of about 5 mo. In temperate areas of southern Australia, rainfall is mostly winter-dominant and summers are dry. More uniform rainfall is associated with subcoastal and coastal areas of south-eastern Australia, but prolonged dry periods can still occur in any season.

Rainfall in Australia is characterized by being not only low but also extremely variable both spatially and temporally. Periods of severe or prolonged drought alternate with periods of flood rains. In between these extremes, most of the rain that does fall evaporates without directly affecting plant growth: in the Broken Hill area of New South Wales (Fig. 1), only 30% of the 200 mm median annual rainfall actually falls in amounts sufficient for plant growth.

In this paper we discuss the main adaptation seen in the four main pest species of Acrididae in Australia, the Australian plague locust, the small plague grasshopper, the spur-throated locust and the migratory locust, as well as other acridid species: adaptations to an environment where the major limiting factor is rainfall.

Australian plague locust, Chortoicetes terminifera (Walker).— The Australian plague locust is the most economically important locust species in Australia (Wright 1987). Outbreaks requiring control are frequent and, in eastern Australia, have occurred in 18 of the 26 y from 1976 to 2001. It is a multivoltine species with 3 to 4 generations per year possible when widespread rain occurs in all seasons. This species is very well adapted to surviving in the subtropical semi-arid areas where rainfall is slightly summer dominant and where there are long lasting grasses, such as *Astrebla* spp. and *Aristida* spp.

Outbreaks of the Australian plague locust usually originate in the arid zone of the Queensland Channel Country and far northern South Australia and New South Wales (Fig. 2). From these inland areas, outbreaks can potentially spread into any of the agricultural areas of eastern Australia, depending on subsequent rainfall and the pattern of migration. Sometimes breeding can also occur in the arid areas of Western Australia, giving rise to a plague in that State. Rainfall is low in the arid zone but long-lasting grasses are common there, so that when enough rain falls to stimulate sustained growth, the plague locust can complete an entire generation before the vegetation dries off again. In some habitats, such as the stony downs, a fall of only 20-25 mm is sufficient for a sustained grass response (Hunter 1989a, Hunter & Melville 1994).

What are the adaptations of the Australian plague locust for survival in the arid interior? Firstly, the eggs can enter quiescence at two different stages of development if conditions are too dry for development to proceed (Wardhaugh 1980). Quiescence stage 1 (Q1) can occur once the eggs have reached 25% development and Q2 can occur after the eggs have completed diapause. Quiescent eggs can survive the winter and, in the interior, some can survive 2-3 mo during the summer. Only a few seem to survive summer without rain, but such survival may be important in allowing locusts to survive prolonged droughts.

During autumn, eggs and nymphs of the Australian plague locust can enter diapause. Egg and nymphal diapause prevent adults being present during the winter when conditions are normally dry and are too cool for night migration. In the subtropics, eggs laid in late March or early April hatch but the nymphs enter diapause as midinstars in mid-April provided they have not already developed past this stage (Wardhaugh 1980). Midinstar nymphs in diapause resume development in late winter and reach the adult stage by early spring when temperatures are again warm enough for night migration. Eggs laid in moist soil from mid-April onwards enter embryonic diapause. The diapause ends about 7-14 w after laying, after a period of cool temperature (10-15°C) (Hunter 1989b). Even during winter, it is always warm enough for egg development in the subtropical arid inland, but rainfall is limiting: eggs resume development when rain falls and moistens the soil.

In addition to being able to avoid dry conditions (egg and nymphal diapause) or to survive when it is dry (egg quiescence), the Australian plague locust has an adaptation to locate areas favourable for breeding: long distance migration. Migration allows the location of suitable areas (open plains with green vegetation) in an environment where rainfall is highly unpredictable and spatially variable. Migration may also be a mechanism for escaping intraspecific competition for limited resources and for escaping the effects of predators, parasitoids and pathogens. The Australian plague locust is a highly mobile species that frequently undertakes long distance night migrations. As the vegetation is drying off, young adults of the Australian plague locust accumulate fat for migration (Hunter *et al.* 1981) and take off after sunset when it is warm and windy with temperatures at 25°C or more. Several hundreds of kilometres may be covered by night migrations with shorter distances (rarely more than 20 km) travelled during the day (Wright 1987).

Locusts will continue to migrate until they encounter an area of recent rain or until they run out of fat. Migration is not always successful and during major locust outbreaks reports of locusts out at sea or being washed up along the beaches of southern Australia are not uncommon. For example, following a major outbreak in South Australia during 2000, billions of dead locusts were detected in Lake Frome, South Australia, using imagery from new satellite equipment being tested by CSIRO.

All of these adaptations enable the Australian plague locust to survive in arid areas with slightly summer-dominant rainfall. The presence of long-lasting grasses ensures that nymphs that hatch out after rain will survive to become adults. However, this species is less well adapted for surviving in the temperate agricultural areas where rainfall is more winter dominant and where long lasting grasses are rare. While the embryonic diapause allows the eggs to escape the cool winters, and spring rains usually enable hatching, summers are usually dry in the agricultural zone, leading to population collapse (Wright 1987). Even though locusts are likely to die out as adults without laying, control of populations that reach the agricultural zone is important because significant crop damage can occur before the outbreaks collapse.

During some seasons, summer rain does fall in the agricultural zone, which can either extend the period of outbreaks that have begun in the interior or even lead to outbreaks with only limited contributions from the interior. In addition, migration from the agricultural zone back into the interior sometimes occurs in spring and may be more important than previously thought (Wright 1987) in sustaining locust populations in source areas.

Small plague grasshopper, Austroicetes cruciata (Saussure).— The small plague grasshopper is a species that has adapted to areas of temperate southern Australia that have moderate

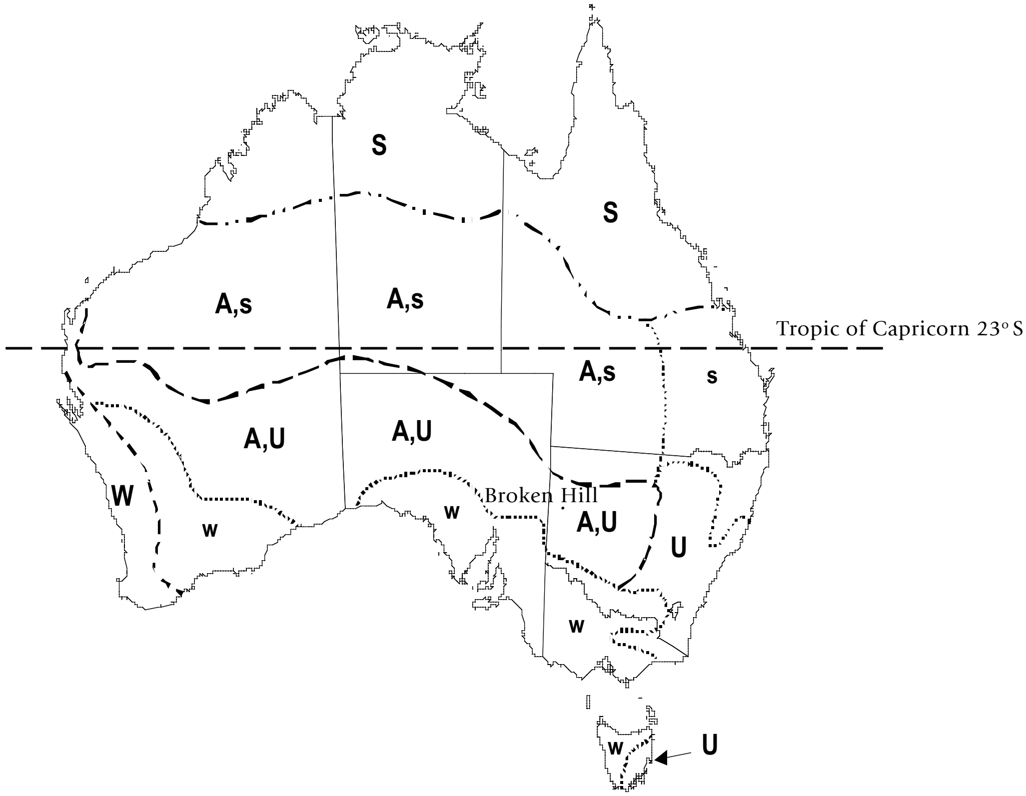

Fig. 1. Main climatic zones of Australia based on rainfall only, adapted from the Bureau of Meteorology (2001). S = summer-dominant rainfall; s = mostly summer rainfall; A,s = arid, mostly summer rainfall; A,U = arid, uniform rainfall; U = uniform rainfall; w = mostly winter rainfall; W = winter-dominant rainfall.

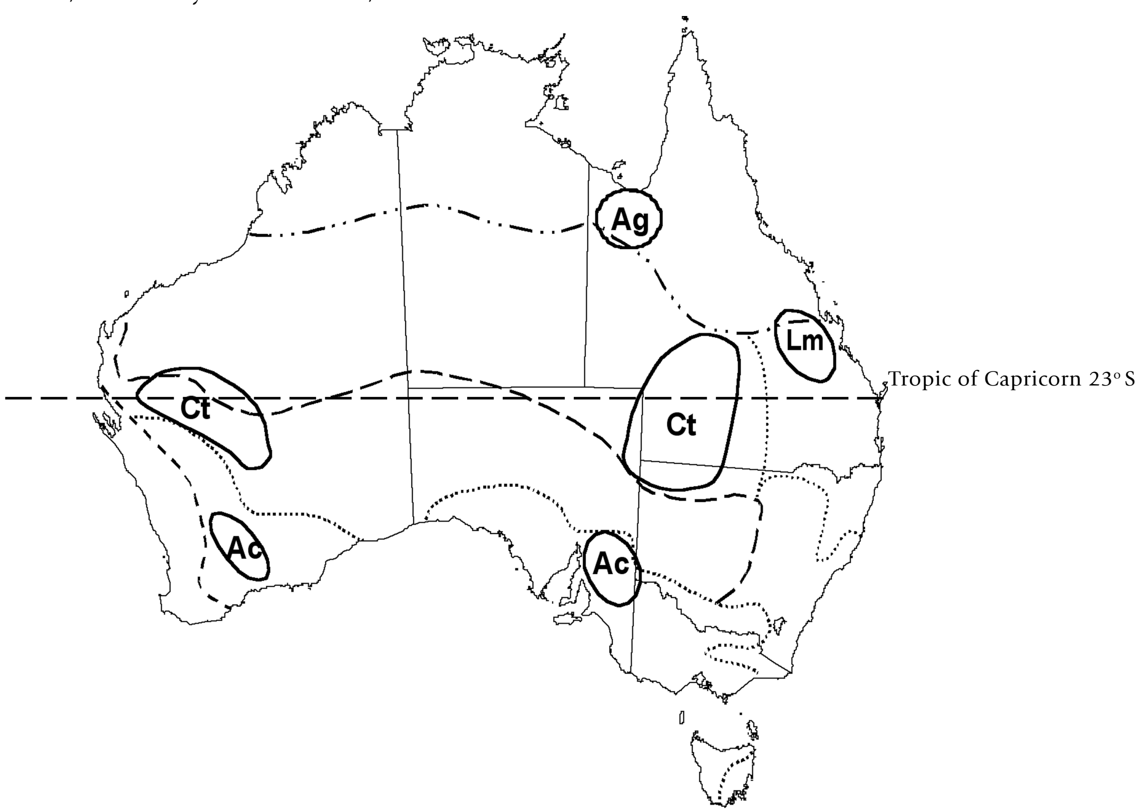

Fig. 2. Main source areas of breeding for the spur-throated locust (Ag), migratory locust (Lm), Australian plague locust (Ct) and small plague grasshopper (Ac), in relation to the main rainfall zones in Australia (see Fig. 1 for a key to the rainfall zones).

winter rainfall and dry summers. It is univoltine, with a generation during spring that reproduces before the onset of the dry summer. The long dry summer is survived in the egg stage that has an 8-9 mo diapause, broken by cool conditions of the next autumn/winter (Andrewartha & Birch 1954). The absence of breeding from midsummer until early winter limits the area that can be infested to where rainfall is winter dominant both in western and eastern Australia (Fig. 2). The small plague grasshopper has a low migratory capacity, with movement limited to some localized day flight. However, even though outbreaks are usually localized, they can cause severe damage to pasture and winter cereal crops over substantial areas, as seen in South Australia during the 1997/98 and 1998/99 seasons.

The exact cause of the locally developing outbreaks of the small plague grasshopper is still not fully understood, but it is probably similar to that of the wingless grasshopper (*Phaulacridium vittatum* (Sjostedt) (Baker 1993), in that too much or too little rainfall is detrimental. Low winter rain limits the spring flush of growth and nymphs die, while too much rain results in a higher population of pathogens or parasites and increases the density and cover of vegetation. Outbreaks develop after several years of moderately dry conditions that reduce parasitism and provide plenty of bare ground for rapid grasshopper development. The collapse of outbreaks has also been associated with the return of high rainfall or severe drought.

Spur-throated locust, Austracris guttulosa (Walker).— The spur-throated locust is adapted to the open plains of tropical northern Australia. Northern Australia has a monsoonal climate of heavy summer rains and a long winter dry season. Locusts survive the dry winter as immature adults in reproductive diapause and they mature after feeding on the green vegetation present at the onset of the wet season. The early rains of the wet season are patchy and adults locate the resulting localized areas of green vegetation through migration. Locusts feed on the short ephemeral grasses, mature their eggs and oviposit; but survival of offspring eggs and young nymphs is assured only if there is further rain within 6 w (Hunter & Elder 1999). By the time nymphs are midinstars, it is usually the height of the wet season, and in the higher-rainfall outbreak areas, rain falls at regular intervals, ensuring survival to the adult stage.

The source area for outbreaks is usually the open grassland plains south of the Gulf of Carpentaria in tropical Queensland (Fig. 2), where regular summer rain ensures survival. But rainfall in the early wet season is localized and many migrating locusts do not find rain areas within the source area and are carried on weather systems to the arid zone; here rain for nymphal survival is not common, leading to substantial mortality. Consequently, any increases in numbers in the outbreak areas are usually balanced by mortality of offspring of locusts invading the arid zone. Outbreaks develop when there are regular rains both in outbreak areas and much of the adjacent arid zone. Because the spur-throated locust is univoltine, major outbreaks take several years of favorable conditions to develop. Outbreaks are infrequent and populations have reached plague levels only during 1973-75 and 1996; but when outbreaks do occur they can be intense and severe (Hunter & Elder 1999).

Migratory locust, Locusta migratoria migratoriodes (R. & F.).— The migratory locust is considered to be a man-made pest in Australia, as prior to the 1970's outbreaks were largely unknown. It was not until the widespread clearing of native vegetation in the Central Highlands of Queensland that a serious problem with this species developed (Farrow 1979). This subcoastal tropical to subtropical area (Fig. 2) of grassland and crops has now become the source of outbreaks during periods of moderate rainfall throughout the year. Locusts that invade drier areas to the west and north die out within a few generations. Populations can persist in coastal areas and the migratory locust can be a minor pest of sugarcane, but because of the small area of suitable habitat for breeding (and perhaps higher levels of parasites and pathogens in these higher rainfall areas), coastal areas do not act as source areas for outbreaks.

The migratory locust is poorly adapted to the dry Australian environment as it does not have a stage that can survive dry periods, and so breeding is frequently unsuccessful due to inadequate rainfall, particularly during the winter rainfall minimum. However, good rain during all seasons results in three to four generations produced annually leading to an outbreak. Normally these outbreaks are localized within the Central and Southern Queensland area, as long distance migrations are not common, particularly when regular rainfall provides green vegetation locally. However, this species forms dense bands and swarms that can cause substantial damage to crops unless controlled.

Other acridid species.— There are many other species of acridids that are well adapted at surviving in the arid interior and which usually have an egg stage that is highly tolerant to dessication. They have a very low or no migratory capacity, so that even though populations can increase rapidly when good rains fall, they often collapse when normal dry conditions return.

Conclusion

Rainfall seems to be a major regulator of acridid populations in Australia. This understanding of the relationship between rainfall and outbreaks (Wright 1987, Hunter & Elder 1999) has been used by the Australian Plague Locust Commission (APLC) to forecast when outbreaks are likely to occur so that programs of preventive control can begin early.

The Australian plague locust is the most important acridid pest in Australia because this species has the greatest number of adaptations for surviving in an environment where rainfall is both limiting in quantity and extremely variable, temporally and spatially. Its ability to enter quiescence or diapause during the egg stage, its ability to rapidly increase in numbers, and its ability to undergo long distance migration, means that it can escape adverse conditions and rapidly find areas of good rainfall.

In contrast, the small plague grasshopper is less of a pest as it is univoltine, has low fecundity and is restricted to areas that have cool winters and reliable spring rainfall. The spur-throated locust, although it readily undergoes long-distance migration, is also less of a pest as it is univoltine and because its eggs are not tolerant of dry conditions. The migratory locust is restricted to areas where rainfall is more reliable all year round as this species does not have a stage that can tolerate long dry periods.

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