Temporal Incidence and Sexual Maturation of *Austracris guttulosa* (Walker) (Orthoptera: Acrididae) in Queensland, Australia

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ABSTRACT Life history data for the cyrtacanthacrid locust *Austracris guttulosa* in Queensland were compiled from field observations over the period 1971-1976. Nymphs were present from November to April inclusive and adults throughout the year, with adults from overlapping generations present in January and February. *A. guttulosa* was univoltine, adults remaining sexually immature throughout the dry season (April to October). Sexual maturation was related to the higher temperatures, humidities and day lengths from September/October onwards and resulted in depletion of fat body. Sexually mature adults died out by February.

Introduction

The spur-throated locust, *Austracris guttulosa* (Walker) [formerly *Nomadacris guttulosa* (Key and Rentz 1994)], has long been recognised as a potentially serious pest in northern Australia (Key 1938) and its pest status could increase as cropping expands into outbreak areas. Bullen (1968) reported serious damage in pilot plantings of crops in the Ord River Scheme in Western Australia. The extensive use of insecticide to control swarms and large scale concentrations has been necessary to prevent major losses of crops in eastern Australia (Casimir and Edge 1979; Elder *et al.* 1979). The species is an occasional serious threat to cropping in central Queensland and in the Burdekin River Irrigation Scheme (Elder *et al.* 1979).

A number of authors have studied the phenology of *A. guttulosa* in various parts of Australia (Bullen 1968; Clark 1949; Farrow 1977; Farrow and O'Neill 1978; Jenkins 1945; Weddell 1937) using field and laboratory studies. The studies indicated that the life history of *A. guttulosa* is determined by parameters (humidity, temperatures, photophase) which are dynamic between wet and dry seasons. In a sub-tropical/tropical environment, this would see egg laying commence with the wet, and nymphs found until the end of the wet season. Under conditions of continuing high moisture, oviposition may be prolonged leading to outbreaks.

Elder (1989, 1991) studied the life history and effect of environmental factors on sexual maturation of *A. guttulosa* in the laboratory. Conditions of RH above 55-60%, temperature greater than 32 °C, and a 14 h photophase were all required to obtain minimum time to sexual maturation. At 60-80% RH and a temperature regime of 32 °C (16 h) and 38 °C (8 h), attainment of sexual maturity required a minimum of 7 weeks after fledgling. Critical photophase was estimated at approximately 13 h. Sexual maturation was greatly accelerated by high relative humidity where temperature was high and by a long photophase (Elder 1991).

This paper reports on a 5-year field study of the temporal dynamics of spur-throated locust life history and reproductive status, complementing the laboratory experiments. Since fat body (the major resource of stored energy) increases rapidly post fledgling but may decrease with egg development or with long periods of flight in other species (Uravov 1966), adult fat body development was studied in conjunction with sexual development investigations.

Materials and methods

Incidence of nymphs and adults of *A. guttulosa* was assessed in the field from October 1971 through to November 1976. Regular collections were made from a study area at Barmount (22° 32′S, 149° 06′E). Supplementary collections were made with the assistance of officers of the Department of Primary Industries and local residents throughout Queensland. Two major surveys were undertaken in November and March each year, at times when previous literature and preliminary studies indicated that changes in sexual maturation or life history stages were expected. Collections starting 1 November each year were made at 160 km intervals along the route indicated (Fig. 1); at the same 21 locations each survey. Collections in March were made at 10 locations along the second route (Fig. 1).

The locations sampled were designated as arid or non-arid using a map ("Land system surveys of the Australian arid zone"—Division of National Mapping, Department of Minerals and Energy) in which the arid zone boundary line (Fig. 1) was based on the moisture index of Fitzpatrick and Nix (1970) (W. F. Mawson pers. comm.). This non-arid zone was further divided into coastal (within 50 km of the coast) and sub-coastal categories on the basis of distance from the coast. This division relates to mean rainfall, evaporation and RH% at 1500 h for October. For example, coastal Mackay has rainfall of 46 mm, evaporation of 200-250 mm and 65% RH while sub-coastal Emerald (about 270 km from the coast) has 42 mm rainfall, 300-350 mm evaporation and 31% RH.

Collection methods. Specimens of locust nymphs and adults were obtained by sweep netting using a standard 457-mm diameter black net. When populations were low and ground cover sparse it was necessary to stalk and capture adults individually after they were flushed by sweep netting. Sampling continued for a maximum of 30 min or until 13 males and 13 females (nymphs and/or adults) had been obtained. In the first 6 months of the study, specimens were killed by freezing. Subsequently, specimens were placed directly into a mixture of 80% ethanol, 3% glacial acetic acid and 17% water to ensure adequate tissue fixation.

Dissection. Using knowledge from laboratory studies (Elder 1989, 1991) and field experience, adults were assigned to new or previous generation according to the hardness of the exoskeleton, and the presence or absence of blue colouration and degree of tatter of their wings. Internal organs were examined to determine state of sexual maturation and development of the fat body. This was accomplished by making an incision along the mid-lateral line on each side of the abdomen and across the dorsal surface of the abdomen between the two tympanal organs, then peeling the dorsal exoskeleton away to reveal underlying structures.

Measurements. The age distribution of nymphs at each site and collection time was assessed using vernier callipers to measure the length (± 0.1 mm) of the hind femora (Elder 1989). Sexual maturity in females was assessed by measuring oocyte length, using a micrometer eyepiece in a binocular microscope (accuracy ± 0.02 mm); In males the accessory glands were rated as immature (1), or mature (2) (Elder 1991). Fat body development was classified as: 0—none detectable between the abdominal organs; 1—few strands present but all abdominal organs clearly visible; 2—numerous strands present and beginning to obscure abdominal organs; 3—strands tending to form sheets and obscure the abdominal organs; 4—fat body forms virtually a continuous dorsal sheet, obscuring the abdominal organs.

Temporal differences in the age distribution of nymphs and sexual maturation of adults were examined graphically in bulk, and compared across zones.

Analyses. An ANOVA model was used in which there were terms for year, sex and location (zone) and the year × sex, the year × location and the sex × location interactions where locations were designated arid, sub coastal or coastal as described above. Data were analysed (ANOVA) separately for each sex to test for differences in sexual maturity between locations and years.

Results

A total of 597 collections were made, totalling 8,615 locusts (4,466 males and 4,149 females) as follows: 1971 (227); 1972 (681); 1973 (2,271); 1974 (2,745); 1975 (2,269); 1976 (422). *A. guttulosa* was collected in areas which included both very high average annual rainfall (Tully 2,000 mm) and low rainfall (Boulia 257 mm) (Fig. 1). Specimens were usually more plentiful among denser and taller vegetation e.g. around waterholes or along stream banks than in sparse or short vegetation. Incidental collections showed similar temporal incidence, maturity or fat body patterns to collections at the November and March survey locations or the regular sampling location at Barmount.

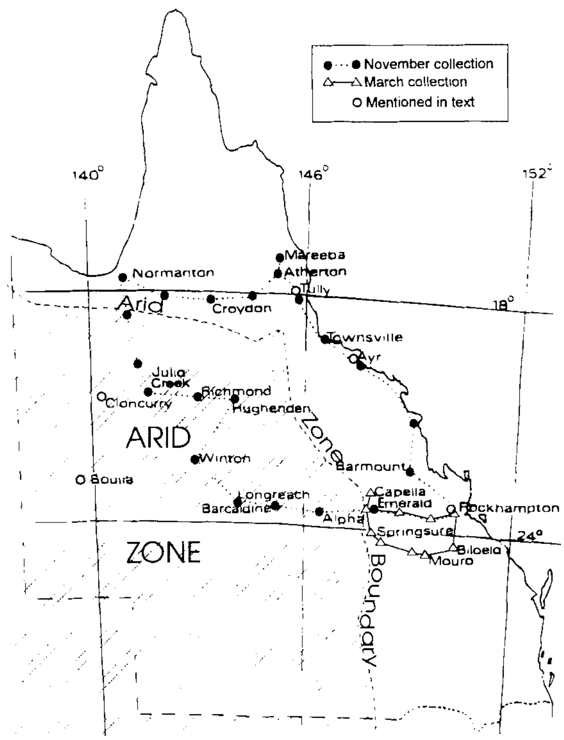

Fig. 1. Collection sites in Queensland and localities mentioned in text.

Temporal incidence. Nymphs were collected from November to April each year between 1970 and 1976. The proportion of older nymphs as indicated by length of hind femora increased through the November to April period (Fig. 2). By 1 April, the majority were fully grown. Adults were present throughout the year. Old adults derived from nymphs of the previous summer could be readily separated from fledglings; by an overall darker (often blue-tinged) colour, a much harder cuticle, tattered appearance, and sexual maturity.

Sexually immature females were collected throughout the year with the lowest proportion of immatures in December. Sexually mature females (oocyte length > 1.0 mm) were collected in the field from 21 September to 22 February and sexually mature males between 7 August and 8 March (Figs

3 and 4). Both sexually mature parents and immature progeny were present in January and February for females (Fig. 3) and from January to March for males (Fig. 4). The small number of sexually immature females present in December could have been from either generation (Fig. 3).

Sexual maturation. Both sexes showed differences in time of sexual maturation, both in different locations in the same year and in the same location in different years. This was particularly noticeable in oocyte length of females collected from different zones during the November field trips (Fig. 5). There was a significant ($P<0.05$) zone × year interaction for oocyte length, which increased for females in the arid and sub-coastal zones in 1975 relative to the preceding years whereas, in the coastal zone, mean oocyte length increased from 1972 to 1973 and remained high in 1974 and 1975 (Fig. 6). Males tended to mature earlier than females and most were mature when collected in November (Fig. 4). There were small highly significant ($P<0.01$) differences between zones with a greater proportion of maturity in males from the coastal zone than sub-coastal males and similarly for sub-coastal compared with arid-zone males. Least square means for the three zones were coastal 1.982, sub-coastal 1.947 and arid 1.928. Years were not significant ($P>0.05$).

Examination of rainfall data for September and October and total rainfall for both months at locations as close as possible to November collection sites, indicated a possible relationship between rainfall and mean oocyte length (compare Figs 5 and 7). Regression analysis of oocyte length on rainfall (square root transformation) for arid, sub-coastal and coastal locations showed significant relationships of oocyte length to September rainfall in arid locations ($R^2 = 0.126$; $P<0.05$); and to October rainfall in coastal

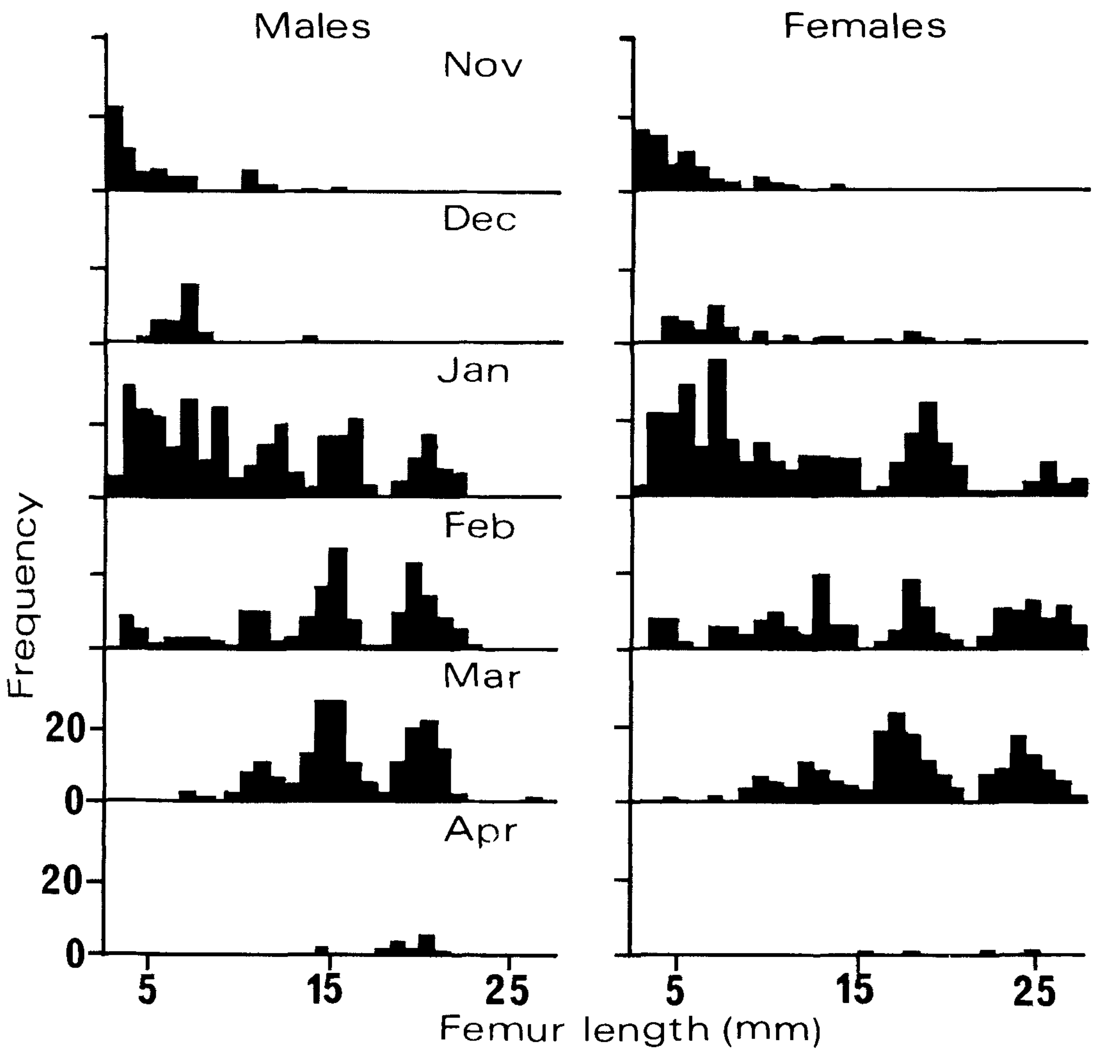

Fig. 2. Monthly age distribution of *A. guttulosa* nymphs as indicated by the frequency distributions of hind femur length. Nymphs were absent from May to October inclusive.

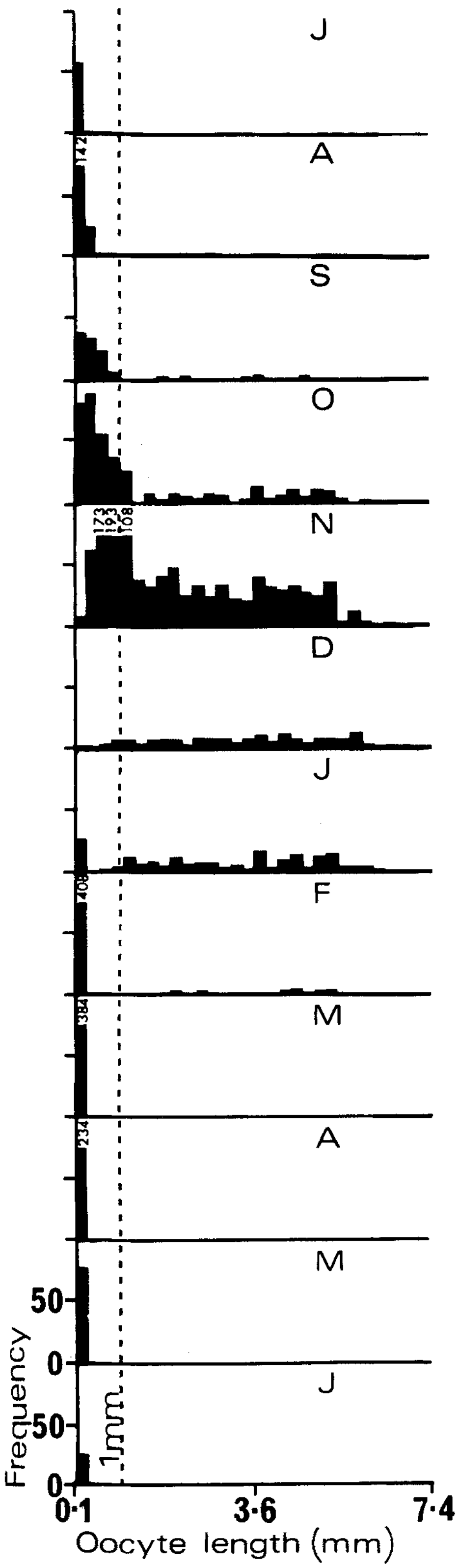

Fig. 3. Monthly frequency distributions for oocyte length for all field collected females. Numbers greater than 100 indicated on the appropriate bar.

locations (R^2 = 0.318; P< 0.01). No other regression was significant.

Rate of sexual maturation in females. Weekly collections at Barmount in September and October 1973 indicated that maturation occurred over 3 weeks from 13 September (Fig. 8). Oocyte length increased at a maximum rate of 1.5 mm per week. On 13 September 1973, the maximum oocyte length was 0.9 mm and 3 weeks later on 4 October 1973 it was 4.6 mm. Forty-six per cent of females were still immature (oocyte length <1.0 mm) at the end of this period.

Fat body. Fat body content of adults was related to month (Fig. 9) and inversely related to sexual maturity (Fig. 3). Throughout the cooler months when the locusts were sexually immature, fat body content was high, with 74% of males and 75% of females rating 4 in August. As sexual maturation commenced in September and continued during October and November, fat body content decreased so that by December 51% of both males and females rated 1. With the death of old adults and the appearance of fledgling adults in January, fat body content was at first low. The proportion of low fat content individuals decreased and high content increased month by month until May when 81% of males and 84% of females were rated 3 or 4.

Although the pattern of fat body content was similar from year to year, the inverse relationship with sexual maturity suggested that there would be differences between years and environments as demonstrated for oocyte length in November (see above).

Fat body rating (P<0.001 for year) decreased from 1972 and 1973 to 1974 and there was an even greater decrease from 1974 to 1975. Fat body rating exhibited an inverse relationship with oocyte length. Fat body ratings (least square means) for 1972-1975 were 2.91, 2.81, 2.03 and 1.44, respectively, and similarly for oocyte length (mm) 1.418, 1.698, 1.735 and 2.207 (P<0.01). Fat body rating was independent of sex (P>0.05) but dependent on location (P<0.001).

Discussion

Temporal incidence. The study confirmed Bullen's (1968) observation that *A. guttulosa* nymphs occur during the wet season (November to April) each year in northern Australia. This occurrence is tied in with sexual maturation of adults (discussed below). The last sexually mature females for the season occurred in February (Fig. 3) and the last nymphs in April (Fig. 2).

Sexual maturation. Males collected annually in November showed only small differences in the average mean maturity (accessory gland rating). This was because the rating system was discontinuous, and there were only two categories, immature and mature. Differences of less than a tenth of a division (0.1) are difficult to evaluate.

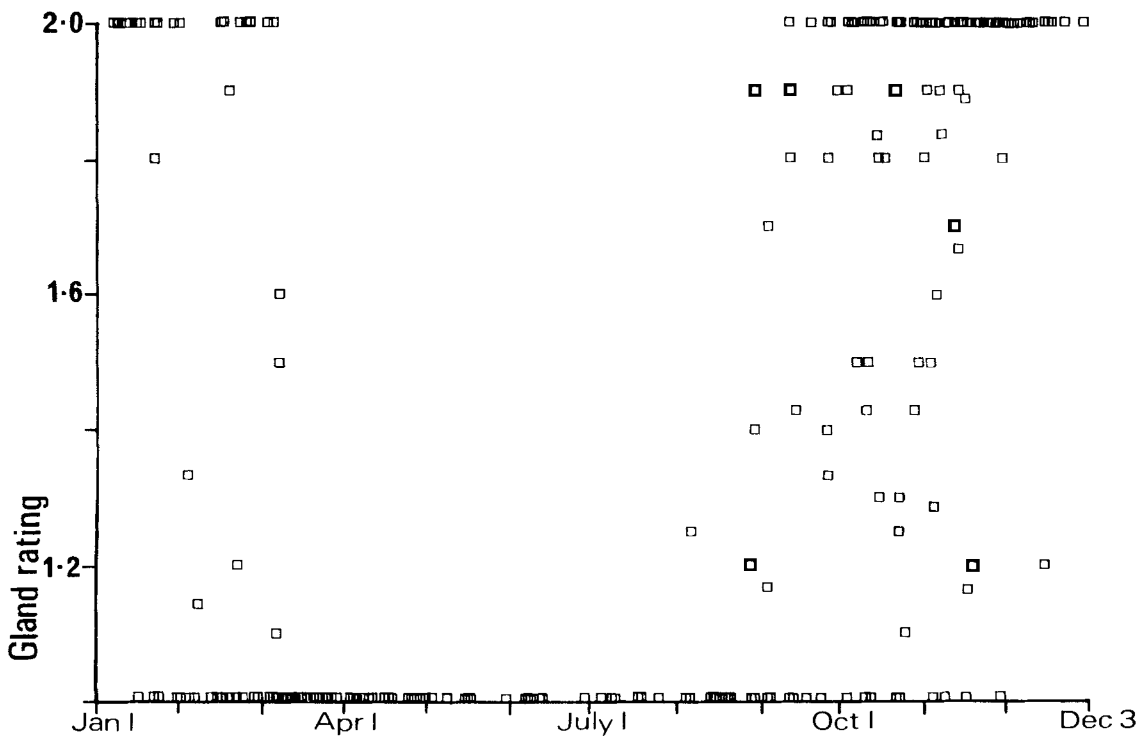

Fig. 4. Mean maturity ratings (1 = immature; 2 = mature) for males for each date and location over the five years (1971-6) of collections.

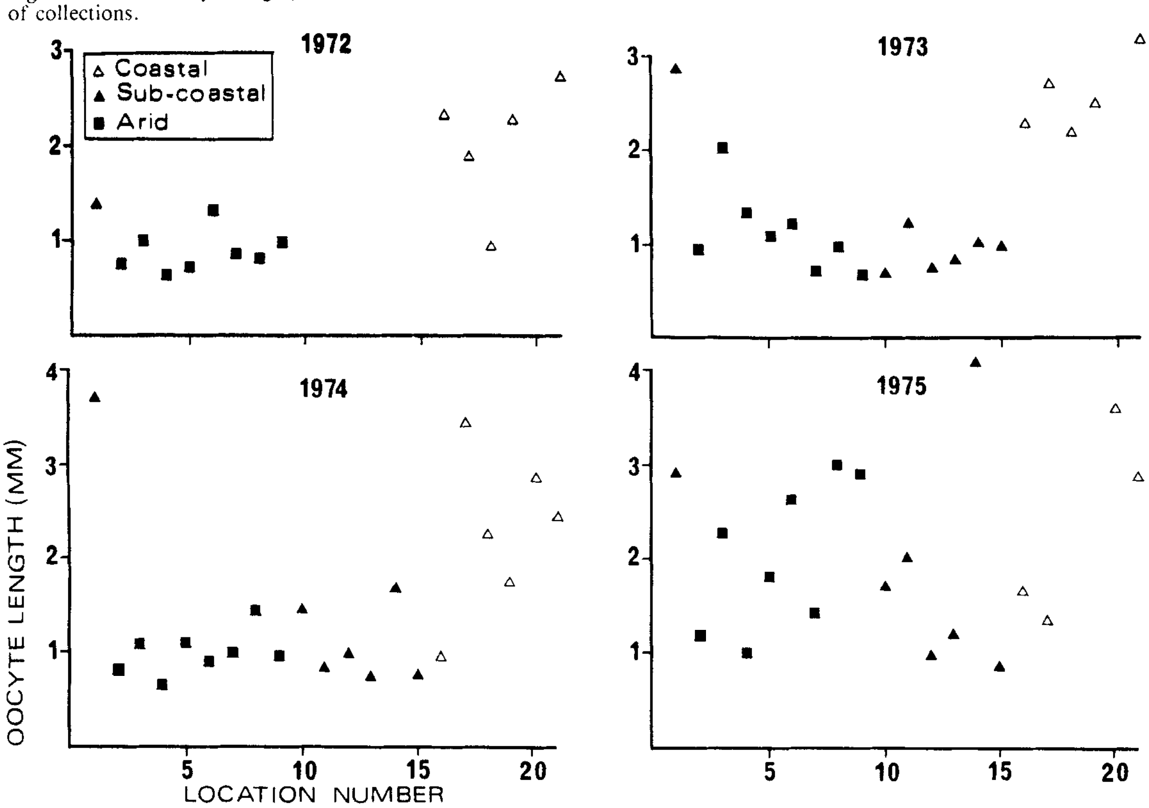

Fig. 5. Annual relationship between location and mean oocyte length in November at 21 collection locations (Fig. 1) numbered consecutively from Emerald—Emerald, Alpha, Barcaldine, Longreach, Winton, Hughenden, Richmond, Julia Creek (JC), 160 km north of JC, 320 km north of JC, Normanton (N), 160 km SE of N, Croydon (C), 160 km E of C, Atherton, Mareeba, 20 km S of Tully, Townsville, 20 km S of Ayr, Mackay (M), Barmount.

The results were similar to those for females with maturity being related to the aridity of the zone. Unlike the females however, sexual maturity in males was not significantly different between years. This was unexpected because of the large differences in rainfall over the 4 years (Fig. 7). Most males had matured before the November collection trip and this could have masked any differences.

Effect of photophase and temperature: A critical photophase of about 13 h estimated by Elder (1991) from laboratory studies correlates with the results of this field study. Sexually mature males and females were taken in the field from 21 September to 22 February, there being one generation per year. Breeding populations of *A. guttulosa* have occurred over the whole of northern Australia (Key 1938) with their southern

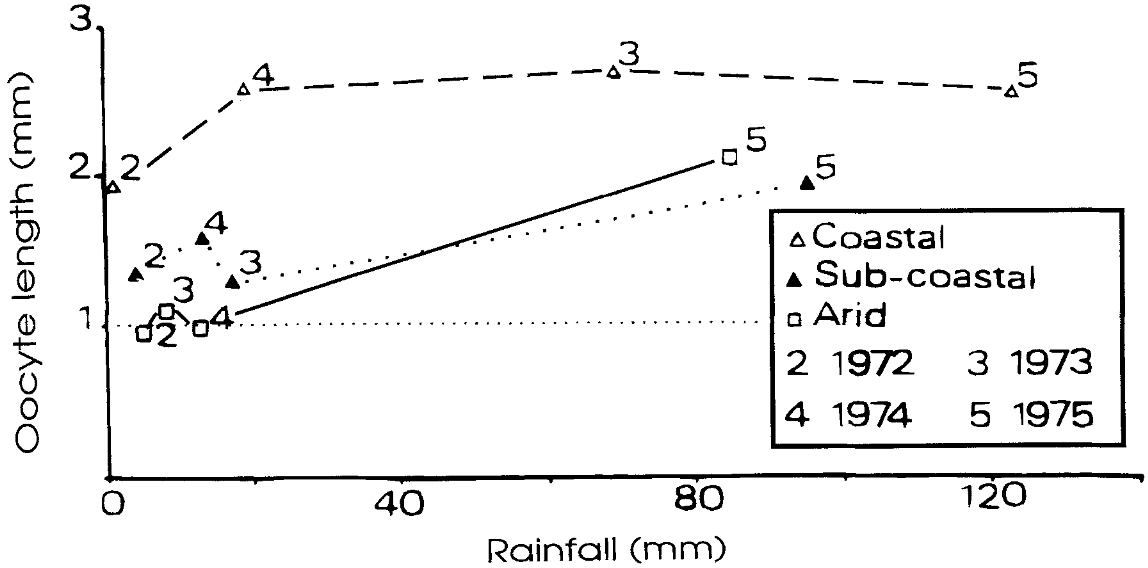

Fig. 6. Relationship between least square mean oocyte length and October rainfall in coastal, sub-coastal and arid zones. Lines connecting means for the same zone are not necessarily in the correct temporal sequence.

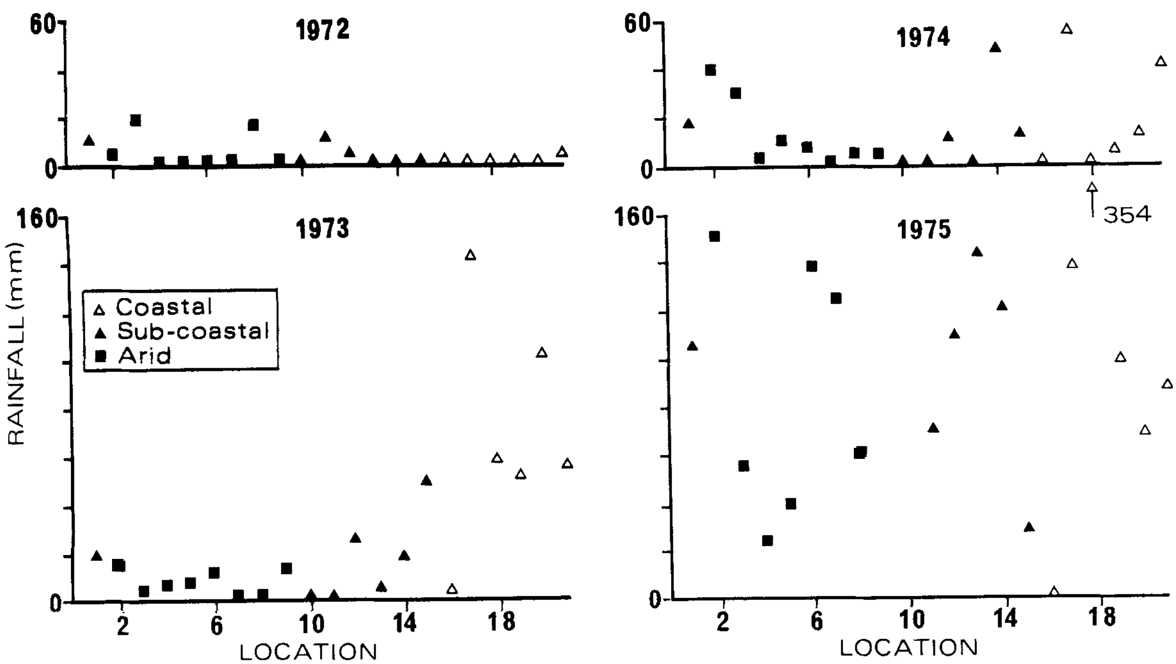

Fig. 7. Relationship between location and rainfall in October. Rainfall stations as close as possible to the annual November locations (Fig. 1). Locations numbered as in Fig. 5.

limits being poorly defined due to mass population movements and variation in movements from year to year. Farrow (1977) recorded successful breeding in the Tamworth region of New South Wales (31 °S) with sexual maturation, as indicated by oocyte length, commencing between 5 and 15 October. A proposed 13 h photophase further is supported by dates of commencement and finish of 13 h photophase and length of the period with photophase of 13 h or greater for four locations. These locations were selected as being representative of the distribution of *A. guttulosa*. They were calculated from tables of first and last light, supplied by the Department of Transport (Australia). They were: Darwin, 12.0 °S 131 °E, 9 Oct. to 5 Mar., 21 wk; Cairns, 17.0 °S 145 °E, 3 Oct. to 10 Mar., 23 wk; Rockhampton, 23.5 °S 150 °E, 27 Sept. to 15 Mar., 24 wk; Tamworth, 31.0 °S 150 °E, 24 Sept. to 19 Mar., 25 wk.

The possibility that over the Australian continent there are geographical races of *A. guttulosa* with different critical photophases is considered unlikely due to the known massive population movements which have been recorded for *A. guttulosa* (Elder *et al.* 1979; Casimir and Edge 1979).

At Guadalcanal (Central Pacific Ocean) where photophase never exceeds 12 h 42 min, sexually mature individuals occur throughout the year (MacQuillan 1976), a situation quite different to that on the Australian continent. The island which lies 9-10 °S and 160 °E, has mean monthly maximum and minimum temperatures throughout the year of 34° and 19 °C respectively and a photophase which varies from 12 h 42 min in January to 11 h 33 min in July (MacQuillan 1976). Further work would be required to elucidate the Guadalcanal situation and relate it to the findings of this study.

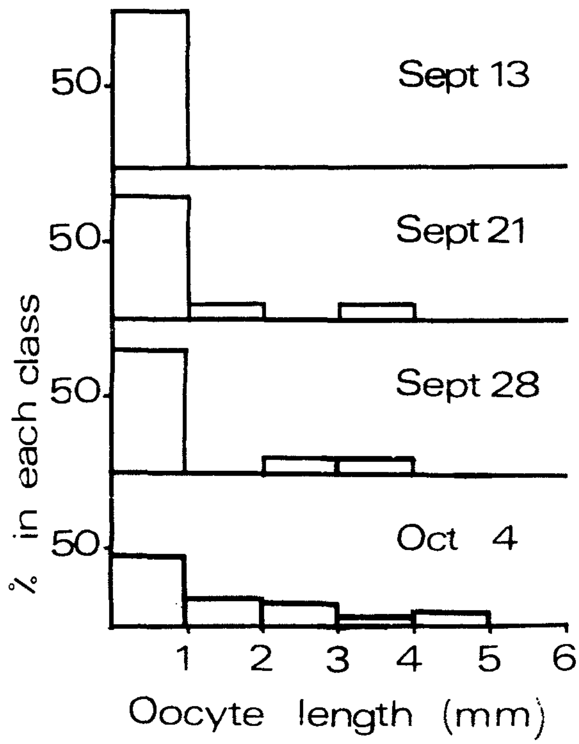

Fig. 8. Weekly frequency distribution of oocyte lengths at Barmount in 1973.

At Rockhampton (23.5 °S, 150 °E), the critical photophase of 13 h is exceeded from 27 September to 15 March. The minimum time from initiation of sexual maturation to 4-week-old adult females of the next generation would be 19 weeks made up as follows: 27 September to oviposition—3 weeks to 18 October, oviposition to hatching—3 weeks to 8 November; hatching to fledgling—9 weeks to 10 January; fledgling until competent to respond to photophase—4 weeks to 7 February; total—19 weeks. i.e. females capable of reacting to photophase could be available by February 7. It is unlikely that these minimum times would be attained in the field. The times were obtained in the laboratory (Elder 1989, 1991) at constant temperatures of 32° and 32°/38 °C whereas average mean, minimum and maximum temperatures (°C) for Rockhampton during October to March (Fitzpatrick 1965) are: October, 23.8, 17.7, 29.9; November, 25.7, 20.0, 31.4; December, 26.9, 21.6, 32.2; January, 27.3, 22.3, 32.2; February, 26.9, 22.2, 31.5; March, 25.8, 21.0, 30.7.

During daylight hours internal temperatures of locusts ranging up to 43 °C have been recorded. These temperatures were well above air temperatures and were achieved by sun basking (Rainey *et al.* 1957; Uvarov 1966; Waloff 1963). In the field the first fledglings appeared in late January (individuals in January with oocyte lengths <1.0 mm in Fig. 3). With a mean temperature of 26.9 °C for February and 25.8 °C for March, it would be most unlikely even with the effects of basking during daylight that sexual development would occur in the 7 weeks to 15 March when photophase dropped below 13 h.

For locations north of Rockhampton, such as Darwin, temperatures would be higher and development faster and partially counteracted by a decrease of 3 weeks in the period over which 13 h photophase occurs, i.e. Darwin 9 October to 5 March compared with 27 September to 15 March for Rockhampton. For areas south of Rockhampton the reverse would apply; temperatures would be lower while the period with 13 h photophase would increase.

Effect of rainfall: The data on sexual maturation from the November field collections showed a relationship between sexual maturation and monthly rainfall. In years with rainfall in October, sexual maturation was much further advanced than in dry years. Similarly sexual maturation was much further advanced in moister coastal environments. Laboratory studies (Elder 1991) showed that the relationship was unlikely to be a direct one, but due to the effect of rainfall on RH. Constant relative humidities of 60% and above were necessary for rapid sexual maturation. During periods of rain, RH approaches 100% and remains high for some time afterwards.

Relative humidity varies diurnally. As temperature decreases in the late afternoon, RH shows a corresponding increase. At Emerald in November for example, on average in any 24 h period RH is above 60% for at least 6 to 9 h. High RH is maintained throughout the night and

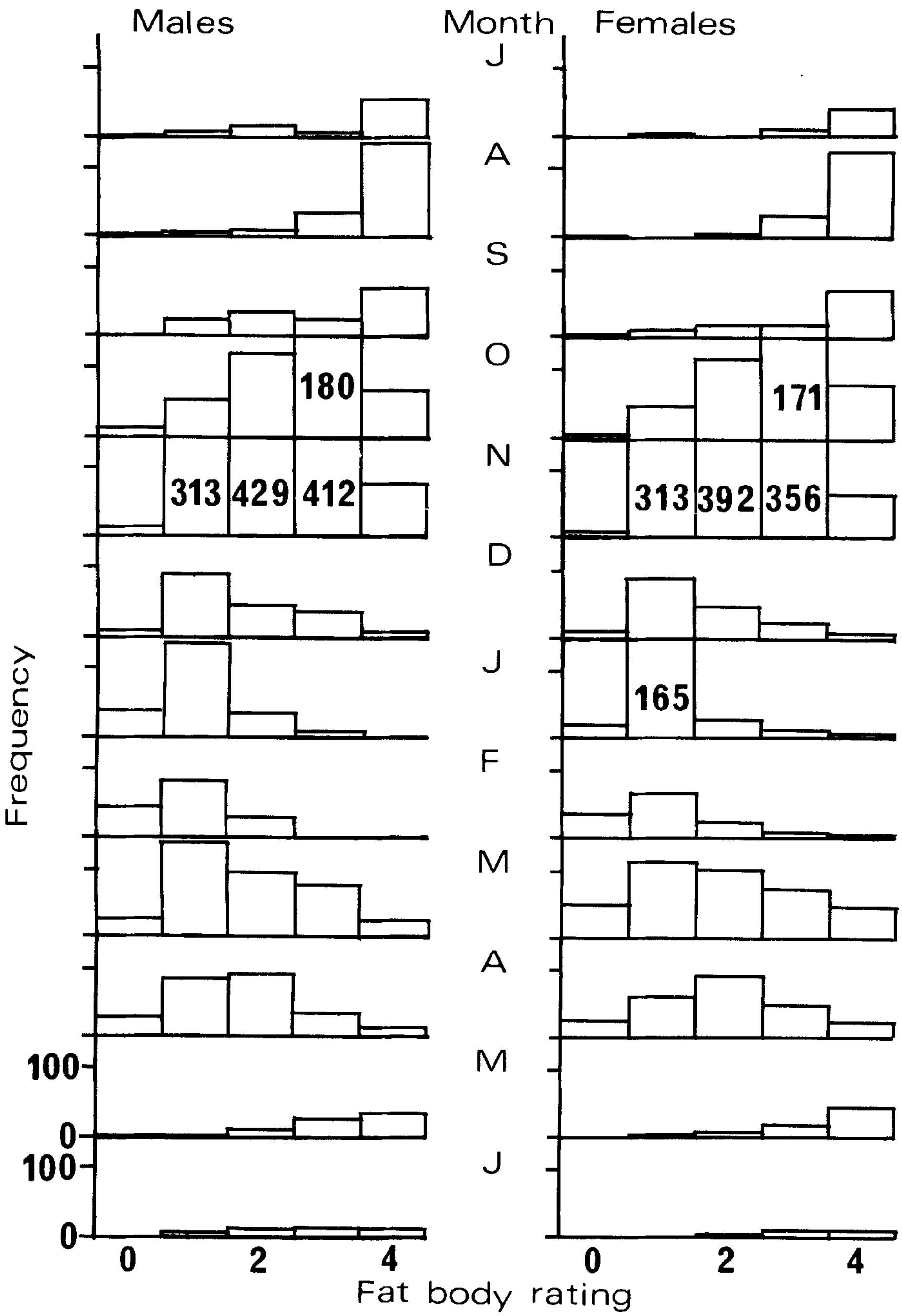

Fig. 9. Monthly frequency distribution of fat body development (graded 0-4) in males and females. Numbers greater than 150 indicated on the appropriate bar.

normally reaches at least 65% (Australian Meteorological Bureau data for Emerald). By 1500 h on a dry sunny day RH can be quite low. Mean monthly RH for Emerald at 0900 h ranges from 53 to 69% and at 1500 h ranges from 31 to 49% (Fitzpatrick 1965).

In an area with a monsoonal climate, RH will be higher in the wet season. Mean monthly RH data for tropical Queensland reflect the effect of the wet season (December to April). During the months of May to August RH at 0900 h may be above the threshold for development (60%) but the accompanying low temperature and short photophase would inhibit reproductive development.

In arid areas such as Cloncurry (20.7 °S and 140.5 °E) (Slatyer 1964) the mean RH can be even lower than for sub-coastal zones such as Emerald (23.5 °S, 149 °E) (Fitzpatrick 1965), and, rarely during daylight hours reach the 60% threshold required for sexual maturation. Cloncurry experiences 2, 3, 5, 7 and 7 mean wet days, respectively, for the 5 months from October to February. Relative humidity could be expected to exceed 60% during these days. In most years sexual maturation/oviposition would be restricted to very limited periods or to moist niches such as along streams. The ovarian cycle may actually be arrested under arid conditions even though a female has laid previously (Farrow 1977).

In the area around the Gulf of Carpentaria while relative variability of annual rainfall (mean deviation expressed as a percentage of annual rainfall) can be as high as 35%, 95% of the annual rainfall of from 700-1,000 mm falls in the period November to April i.e. only 5% outside this. Further south, with the exception of eastern coastal districts, rainfall decreases and relative variability increases along with a proportional increase in the percentage of annual rainfall occurring outside the "wet" season of November to April. Winton for example, has an annual rainfall of 380 mm, a 40% relative variability and 75% falls in the "wet" season i.e. 25% outside this (Dick 1958).

Because of the extreme variability in the amount and incidence of rainfall, the mean rainfall figure and figures derived therefrom for Central Queensland (around 23.5 °S) tend to obscure the extremely erratic nature of rainfall in the region (Fitzpatrick 1965). Under these conditions large variations in populations of *A. guttulosa* occur from one year to the next in the same area (Elder *et al.* 1979). The species has adapted to this situation. By restricting sexual maturation to photophase of 13 h or more the species ensures that oviposition will occur in the warmer summer months when rainfall is more likely to occur and result in growth of luxuriant ephemeral vegetation suitable for rapid egg production, and subsequent nymphal growth and development. It has been shown that high humidities also facilitate maturation (Elder 1991). This association would ensure that sexual maturation was delayed until rainfall occurred or was imminent.

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