Distribution Patterns, Dispersal, Seasonal Abundance and Reproduction of *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae) in the Arid Zone of New South Wales

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The seasonal abundance, local distribution and dispersal of *Chrysomya rufifacies* (Macq.) were studied at the University of New South Wales Fowler's Gap Arid Zone Research Station. This species is abundant from late spring through to mid-autumn and is trapped in greatest numbers at the homestead and in the creek lines, and will disperse throughout these areas if conditions are suitable. The life cycle of *C. rufifacies* from egg to adult takes 9 to 13 days at 27-29°C. It is confirmed that this blowfly produces unisexual offspring.

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INTRODUCTION

Chrysomya rufifacies, the hairy maggot blowfly, is regarded as the most widespread, abundant and harmful secondary fly in Australia (Mackerras, 1933). A species native to the Australasian and Oriental regions (Holdaway, 1933), it has been reported as far north as Japan (Kano, 1958) and during the last decade has spread into Central America and the southern parts of the United States (Guimarães *et al.*, 1979; Gagné, 1981; Baumgartner and Greenberg, 1984; Greenberg, 1988). The hairy maggot blowfly is a subtropical-temperate species and can be found all year round in northern Australia, but it is restricted to the warmer months in its southern range (Waterhouse, 1947; Norris, 1959; Barton, 1982; Monzu, 1979; O'Flynn and Moorhouse, 1979; Anderson *et al.*, 1984a). Dispersal within Australia and local distribution patterns have not been studied.

Adult *C. rufifacies* are metallic green or blue in colour and grossly resemble *Lucilia cuprina* (Wied.), but are distinguishable to the naked eye by dark bands on the abdominal tergites. The larvae average 14 mm in length and are a dirty yellow colour (Fuller, 1934). The second and third instar maggots possess body papillae giving them a characteristic 'hairy' appearance. This tough, 'spiny' skin is thought to protect the maggots from predators (Fuller, 1934).

Chrysomya rufifacies breeds chiefly as a secondary carrion fly (Norris, 1965; O'Flynn, 1983) but may act as a primary carrion fly under some circumstances (O'Flynn and Moorhouse, 1979; Anderson *et al.*, 1984a). The reason for this change in roles is not fully understood. Adult flies can be seen visiting the carcass before decomposition but oviposition does not occur until the primary flies have become established (Fuller, 1934).

The first instar maggots are necrophagous while those of the second and third instars develop piercing mouth hooks and become predacious, feeding both on the carrion and primary larvae already on the carcass (Fuller, 1934; Waterhouse, 1947). *Chrysomya rufifacies* maggots are considered a major competitor of primary fly species on carrion, particularly *L. cuprina* (Fuller, 1934; Waterhouse, 1947; Anderson *et al.*, 1988). Waterhouse (1947) suggested that the high temperatures generated by the overcrowded maggots exert a repellent effect on the primary larvae, forcing them to leave the carcass even before they have finished feeding.

The life cycle of *C. rufifacies* is briefer than any other carrion species. Pupation occurs in or on the carcass, or on the soil surface, but rarely underground — leaving the pupae vulnerable to predation and parasitization (Fuller, 1934; Norris, 1959). A cold resistant stage has not been recorded for *C. rufifacies* (Norris, 1965). Mackerras (1933) found that *C. rufifacies* could survive as pupae during mild winters in the subtropical areas but it is unclear if this species overwinters in the colder southern parts of its range (Barton, 1982). Norris (1959) suggested that *C. rufifacies* may migrate from the north every spring.

Chrysomya rufifacies was first found to be associated with blowfly strike in Australia in 1912 (Holdaway, 1933). In the majority of cases this species combines with a primary species such as *L. cuprina*, often exacerbating these strikes and increasing the chance of mortality. These combination strikes account for 1 to 10% of strikes in Australia (Fuller, 1934; Mackerras and Fuller, 1937; Monzu, 1979) with 5% being recorded at Fowler's Gap (Anderson *et al.*, 1989).

The aim of this paper is to provide details of the seasonal and local distribution of *C. rufifacies* in an arid, sheep grazing area of New South Wales. Aspects of the reproductive biology of this species are also documented.

MATERIALS AND METHODS

Study Area

This study covers part of a programme being conducted at the University of New South Wales' Fowler's Gap Arid Zone Research Station, 110 km north of Broken Hill. The station covers an area of 39200 ha and is climatically representative of much of southern Australia's arid zone (Mabbutt *et al.*, 1972), with an average annual rainfall of approximately 200 mm, evenly distributed over the summer and winter period.

An extension of the Barrier Ranges separates the station into two major areas, the 'hills' and the 'flats or plains'. Several ephemeral creeks run through the area, the main one being Fowler's Gap Creek. The vegetation is classified as chenopod shrubland. During summer, grasses become prominent and in winter, ephemeral forbs. River red gums (*Eucalyptus camaldulensis*) are restricted to the creek line while clumps of *Acacia victoriae* (prickly wattle) are common over the plains.

Fowler's Gap Station increased its merino sheep flock from 5200 in 1984 to 6500 in early 1990. This has been mainly due to the exceptional seasons experienced from 1987 to 1989. The station also runs small numbers of cattle and horses. The red kangaroo is a common inhabitant of the plains along with small populations of both the western and eastern grey kangaroos which concentrate along the creek lines. The euro is restricted mainly to the hills. Introduced species such as rabbits, feral goats, foxes and pigs proliferate in the area.

Sheep blowflies have been studied at Fowler's Gap since 1981. Trapping data collected over the past eight years are available but for the purposes of this paper we use only the periods from May 1984-June 1985 (dry/normal conditions) and January 1989-March 1990 (exceptional/wet conditions). Only the plains population will be discussed.

Weather Data

Rainfall and monthly temperatures were recorded at the Fowler's Gap meteorological station. A hygrothermograph placed in a Stevensons Screen at the meteorological station took hourly temperature readings throughout the blowfly trap runs. This temperature information was used to standardize the trap catches using the method of Vogt (1988).

Seasonal Abundance and Local Distribution

Flies were trapped every two to three weeks using a Western Australian (WA) style trap (Vogt and Havenstein, 1974). Six permanent trapping sites that have been established on the flats (Fig. 1) incorporate different vegetation and landform types (Table 1). The traps were set for twenty-four hours using fresh baits for each run to reduce the possibility of variation in attractiveness of the bait (Vogt *et al.*, 1983). The bait consisted of 500g of lamb liver, 1L of water and 40g of sodium sulphide (A.R.).

TABLE 1

Description of trap sites (Anderson, 1984)

Trap Site No.	Description
10	Flood out plain, prickly wattle in vicinity, in Mandleman Pdk.
12	Banks of F. Gap Ck, Mandleman Pdk. River red gums and prickly wattle, frequented by stock when fodder growth in channels (after rain).
13	Mandleman bore, permanent water supply, dense shrubs and taller *Eucalyptus* sp., stock yards, regular watering point for sheep and kangaroos.
14	Plains in Saloon Pdk, sparse vegetation no permanent water nearby.
20	Banks of F. Gap Creek in Saloon Pdk, similar vegetation to site 12, water trough 1 km away.
17	Homestead, near killing shed and offal pit, in vicinity of shearing shed, sheep yard, pigpen, dog kennels, rubbish dump, horse stalls and houses. Permanent water, various native trees (mostly *Eucalyptus* spp.), flowers and grasses in gardens.

Local distribution was also studied with mark/release experiments. The blowflies were marked with fluorescent dust using the method of Norris (1957) and released after dusk to minimize handling problems (Vogt *et al.*, 1981). A grid of fifteen Williams traps (Williams, 1984), 500m apart, was set up around the release site and checked every twenty-four hours for three days. The six permanent WA trap sites were set twenty-four hours after release and checked for three days.

Life Cycle and Reproduction Experiments

These experiments were conducted in laboratories at the Centre for Entomological Research and Insecticide Technology (CERIT) and Fowler's Gap. At CERIT flies were kept in constant temperature (CT) rooms at 27°C ±1.5°C, with a light regime of LD12:12 and uncontrolled humidity (water was allowed to evaporate naturally from uncovered containers in the room). In the CT room at Fowler's Gap the temperature ranged between 25°C and 30°C, with similar photoperiod and humidity conditions.

The flies were kept in cloth cages and given water and sugar cubes *ad libitum*. Females were allowed two protein feeds in the form of sponge soaked with lamb's blood and the larvae were raised on a mixture of beef mince and bran. The prepupae were encouraged to leave the beef mixture by gradually wetting it, so they would pupate on or in the sand provided.

The females were 'egged' in individual 20 mL glass tubes, in which a moist piece of sponge and a small amount of minced beef was placed. The number of eggs each female laid was determined by first immersing the egg mass in water so they could be separated and counted.

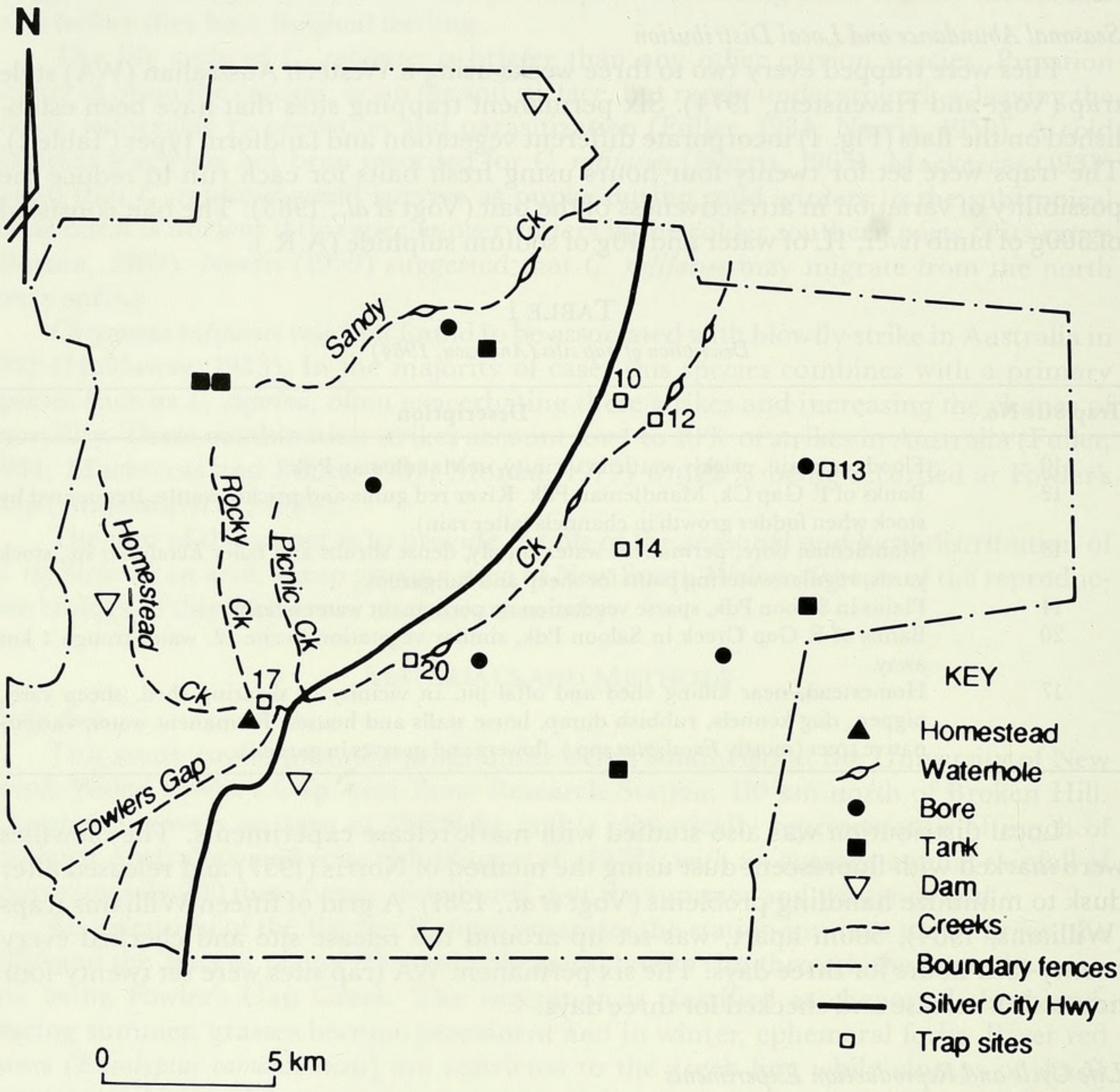

Fig. 1. Map of the Fowler's Gap Research Station showing the main creek lines, water supplies and location of blowfly trap sites.

Statistical Analysis

All fly trapping data were converted to an hourly catch rate (HCR) per trap. For the analysis of seasonal catch variability, an average HCR for the six trap sites (a 'trap run') was calculated. The distribution of trap catches was found to be non-normal so the data were analyzed using the Kruskall and Wallace nonparametric analysis of variance and the nonparametric multiple comparisons test by STP (Sokal and Rohlf, 1981). The average HCR between seasons was compared to establish if there was a seasonal trend, with each trap run as a replicate. The HCR's at each of the trap sites within a season were compared to establish if there was a preference for certain trap sites (i.e. habitat preference).

RESULTS

Weather Data

Fowler's Gap was extremely dry in 1982 (annual rainfall 94 mm) and for the first nine months of 1983 (rainfall 139.3 mm). Heavy rains fell in late spring and summer of 1983/84 (Oct.-Feb. 238.9 mm) which provided excellent vegetation growth. Only a further 120 mm fell throughout 1984, with the last two months of the year becoming very dry (Nov.-Dec. 7.5 mm). The dry conditions continued into 1985 until late autumn (Fig. 2).

Rainfall was above average in 1988 (273.2 mm) and 1989 (336.1 mm) resulting in exceptional vegetation growth. Temporary water holes in creeks and paddocks were present for a large part of the time. Winter 1989 was the coldest on record since 1982, with the average ground minimum dropping below 0°C in August (Fig. 3). Only light rain fell in spring and summer 1989/90 (Sep.-Feb. 76.7 mm) and by autumn 1990 the vegetation had dried off and surface waters had significantly decreased.

Seasonal Abundance

The general pattern of *C. rufifacies* population size is an increase in spring rising to a peak in late spring or early summer, followed by a decline in late summer recovering slightly with a smaller peak in autumn, and then virtually disappearing over winter. This pattern is evident in both the raw and standardized trap data. Although more females were trapped than males, both sexes follow a similar pattern.

The distribution of *C. rufifacies* caught in traps in 1984/85 is shown in Fig. 4. From low numbers throughout winter 1984, the population increased in spring reaching a major peak in early summer then decreased rapidly in late summer. The population recovered in mid-autumn only to decline again in winter 1985. The average HCR was nearly significantly different between seasons ($\chi^2 = 7.815$, $P<0.07$).

The pattern for 1989/90 was similar (Fig. 5). In mid-autumn there was a small peak in the *C. rufifacies* population but the species was not trapped in winter 1989. The population did not increase until mid-spring and reached a major peak in late spring. The fly numbers trapped at this time were much higher than those of spring 1984. Throughout summer and early autumn the *C. rufifacies* population gradually declined. The average HCR was significantly different between seasons ($\chi^2 = 10.337$, $P<0.05$).

Local Distribution

In 1984/85 there was a significant difference in HCR between sites in winter ($\chi^2 = 13.796$, $n=3$, $P<0.01$) and spring ($\chi^2 = 8.998$, $n=4$, $P<0.06$), but not in autumn or summer. *Chrysomya rufifacies* was caught in greatest numbers at site 17 (homestead) and site 12 (creek bed) during winter and spring (Table 2). In 1989/90 there was a significant difference in HCR between trap sites in autumn ($\chi^2 = 11.901$, $n=3$, $P<0.05$) and summer ($\chi^2 = 11.600$, $n=4$, $P<0.05$) and again the flies were caught in greatest numbers at the homestead and creek areas (sites 17, 12 and 20). Only two *C. rufifacies* individuals were trapped in winter 1990 and they were caught early in the season (Table 2).

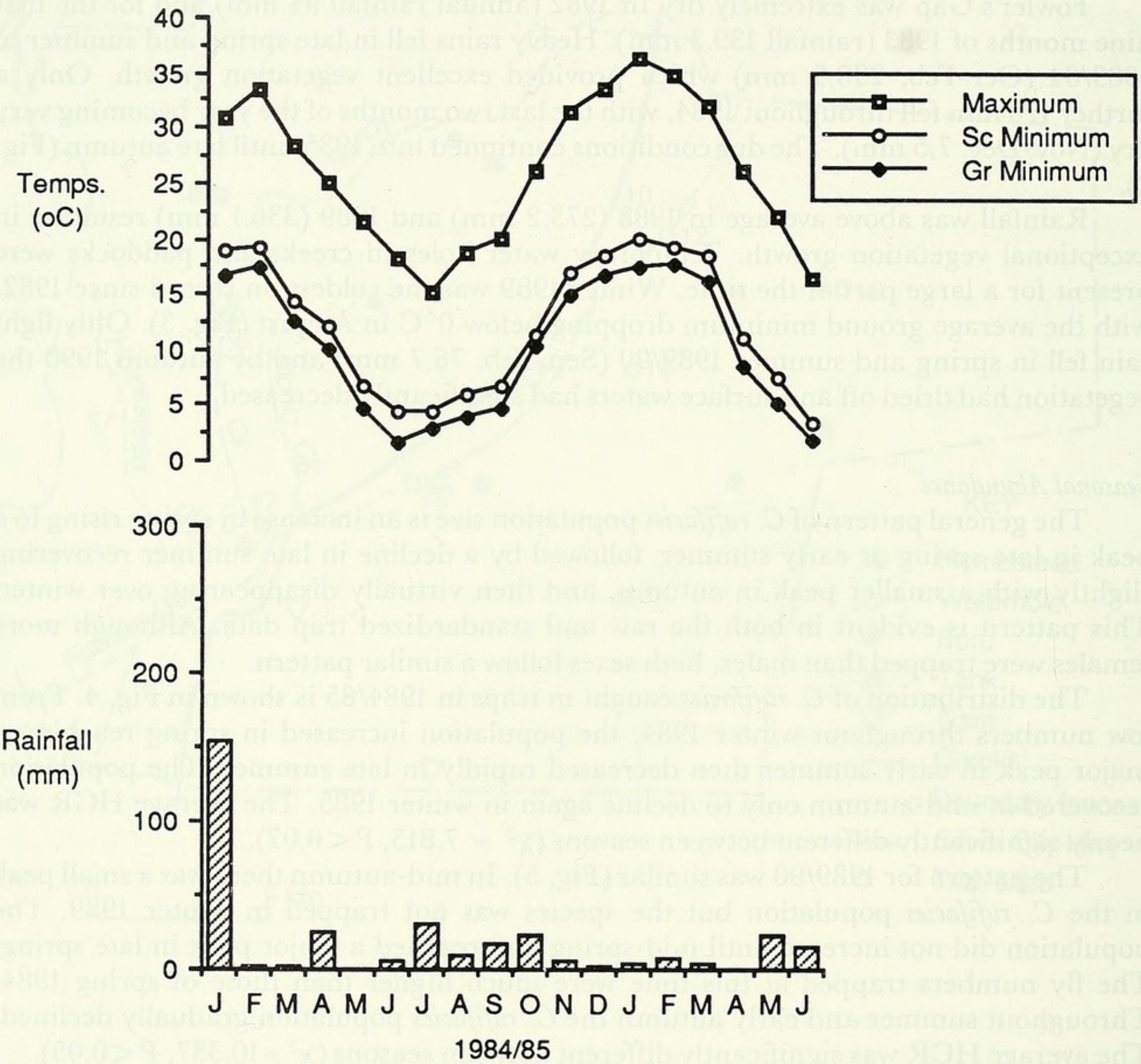

Fig. 2. Monthly rainfall and average monthly temperatures, 1984/June 1985.

Four mark/release trials were conducted (two in autumn, and one each in late winter and mid spring). In all trials the flies were released from site 20, a creek site. In the autumn trials, *C. rufifacies* were mainly trapped at creek sites; the one exception, a female trapped at site 13 (Mandleman bore, 6km from creek) four days after release. Several individuals were caught at site 17 (homestead), five kilometres downstream, after twenty four hours. In the winter and spring releases, individuals were only trapped at the site of release.

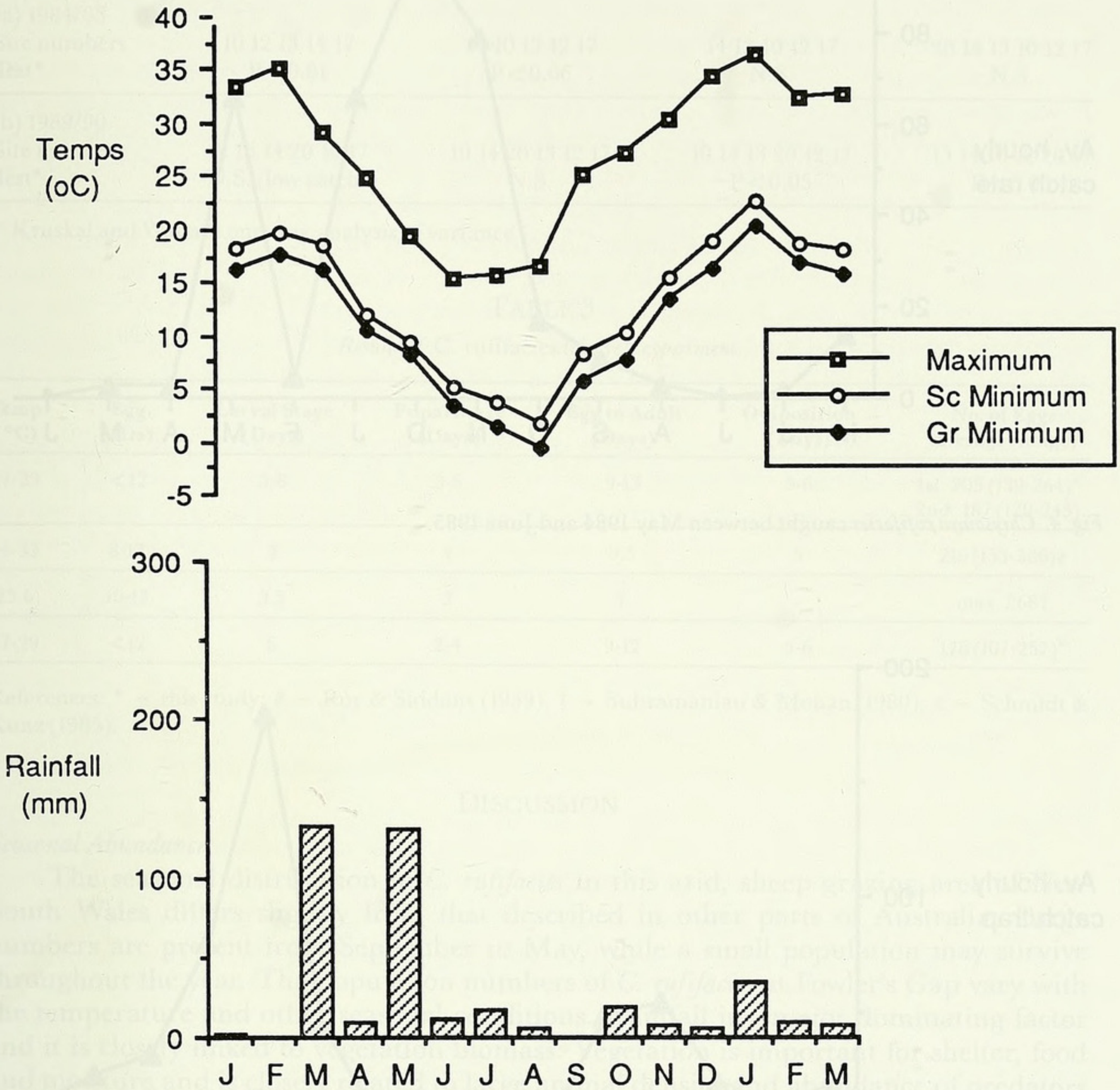

Fig. 3. Monthly rainfall and average monthly temperatures, 1989/90.

Life Cycle and Reproduction

The life cycle of *C. rufifacies* from egg to adult was 9-13 days at 27-29°C. Oviposition took place after 5-6 days but after approximately 28 days females failed to oviposit even though after dissection, many were found to contain fully developed eggs. The results of these experiments are set out in Table 3, with a summary of results from comparable studies.

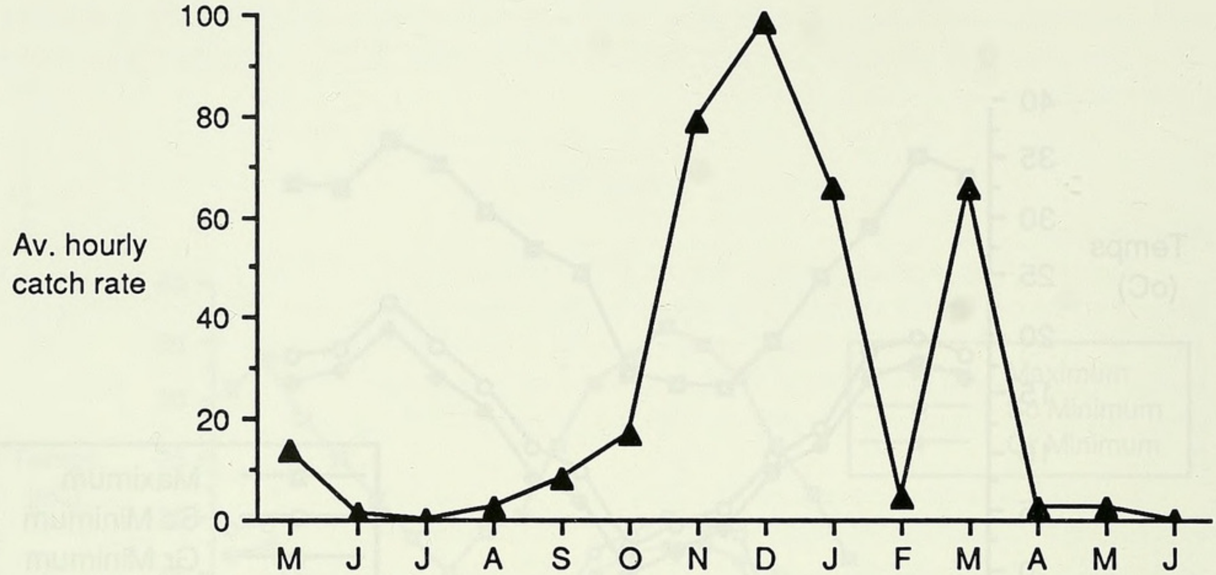

Fig. 4. Chrysomya rufifacies caught between May 1984 and June 1985.

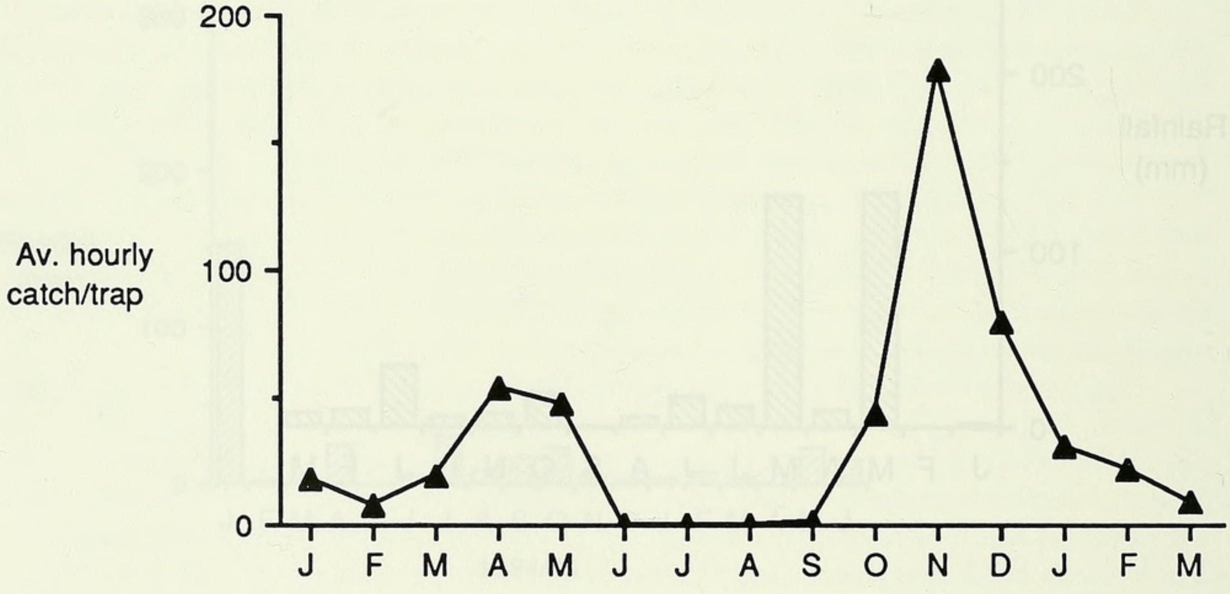

Fig. 5. Chrysomya rufifacies caught between January 1989 and March 1990.

Females tested in the laboratory were able to lay at least three egg batches from one mating. The average number of eggs for the first batch was 205 (range 139-264: n=20) and the second batch was 187 (range 120-243: n=10). Batches laid later were not counted.

As already reported *C. rufifacies* has previously been shown to be monogenic, females always producing unisexual offspring. Our results confirm this with each successive batch of eggs deposited by an individual female always producing the same sex offspring as the first batch.

TABLE 2

Banking of trap catches of C. rufifacies

Catch Period	Winter	Spring	Summer	Autumn
(a) 1984/85				
Site numbers	10 12 13 14 17	14 10 13 12 17	14 13 10 12 17	20 14 13 10 12 17
Test*	P<0.01	P<0.06	N.S.	N.S.
(b) 1989/90				
Site numbers	12 13 14 20 10 17	10 14 20 13 12 17	10 14 13 20 12 17	13 14 10 12 20 17
Test*	N.S. (low catch)	N.S.	P<0.05	P<0.05

* Kruskal and Wallace one-way analysis of variance.

TABLE 3

Results of C. rufifacies *life cycle experiments*

Temp (°C)	Egg (Hrs)	Larval Stage (Days)	Pupal Stage (Days)	Egg to Adult (Days)	Oviposition (Days)	No. of Eggs Average (range)
27-29	<12	5-8	3-5	9-13	5-6	1st: 205 (139-264)* 2nd: 187 (120-243)
24-33	8-12	5	4	9.5	5	210 (153-386)#
25.6	10-12	3.5	3	7	–	max. 268†
27-29	<12	6	2-4	9-12	5-6	178 (107-257)^x

References: * = this study; # = Roy & Siddons (1939); † = Subramanian & Mohan (1980); x = Schmidt & Kunz (1985).

DISCUSSION

Seasonal Abundance

The seasonal distribution of *C. rufifacies* in this arid, sheep grazing area of New South Wales differs slightly from that described in other parts of Australia. Large numbers are present from September to May, while a small population may survive throughout the year. The population numbers of *C. rufifacies* at Fowler's Gap vary with the temperature and other seasonal conditions. Rainfall is a major dominating factor and it is closely linked to vegetation biomass. Vegetation is important for shelter, food and moisture and is closely related to large animal density and abundance of predators and competitors of *C. rufifacies.*

Mild conditions allowed *C. rufifacies* to breed in carcasses throughout winter 1984 (Anderson, 1984) when usually there are insufficient adults to allow breeding and the temperatures are too cold for successful larval development. Population numbers were severely depressed during winter 1989 and *C. rufifacies* did not breed on carcasses during this winter. Only future studies will show whether *C. rufifacies* overwinters at Fowler's Gap or whether it survives in small numbers by breeding on carcasses in protected areas. The migration and movement of this species at Fowler's Gap is also unknown.

Local Distribution

Distribution of blowflies within a habitat is irregular and aggregations of flies are not readily explained (Norris, 1965), although factors such as food, water and shelter would be important (Braack and Retief, 1986). Most flies require water and carbohydrate (Norris, 1959) and *C. rufifacies* females need protein for maturation of their ovaries (Roy and Siddons, 1939). At Fowler's Gap, the sources of carbohydrate would include nectar from flowers and honeydew produced by hemipterans (Anderson, 1984). Protein would be readily available in carcasses, offal and animal faeces. Water is available from stock watering points and waterholes, as well as sweat and saliva of the larger animals and occasionally as dew on vegetation.

Anderson *et al.*, (1984b) found that *L. cuprina* was trapped in greatest numbers at the homestead and creek areas at Fowler's Gap, and *C. rufifacies* also follows this pattern. When a significant difference occurred between trap sites, the homestead (site 17) and the creek areas (sites 12 and 20) always recorded the highest catches of *C. rufifacies*, indicating a preference for these areas. These sites offer a concentration of food resources and protection. Many larger animals are also attracted to these areas to feed and shelter, increasing the potential food resources for the flies. Adult flies are more active in the shade than in direct sunlight (Braack and Retief, 1986), so the flies can spend more time searching for food and mates in the creek beds than in other exposed areas. As shown from the mark/release trials *C. rufifacies* disperse chiefly throughout the creek lines.

As already discussed, the seasonal distribution and abundance of *C. rufifacies* at Fowler's Gap is linked to the seasonal conditions. The local distribution within a season could also be influenced by the number of individuals in the population. The resources in preferred areas would be limited, so once population numbers reach a level at which additional members cannot be sustained (the preferred area population threshold), individuals would be forced into other areas to search for available resources (food, water, shelter or breeding areas).

$$\text{Threshold value} = \frac{\text{population number when individuals begin to disperse}}{\text{quantity of available resources in the preferred area}}$$

The local distribution in seasons with abundant resources differed from those with limited resources. Heavy autumn rains in 1989 generated heavy vegetation growth which survived until early summer. In late spring and early summer 1989 the preferred areas were able to sustain a higher population number of *C. rufifacies* than for the same period in 1984 when conditions were drier, and the vegetation was still recovering from major drought in 1982/83.

Reproduction

Chrysomya rufifacies is the dominant blowfly species from late spring to early autumn at Fowler's Gap. This species is more tolerant of hot and dry conditions than *L. cuprina* or *Calliphora* spp. (Anderson, 1984) because adults can grow and reproduce normally up to 40°C (Waterhouse, 1947) and larvae can tolerate higher temperatures than primary larvae (Fuller, 1934). *Chrysomya rufifacies* is restricted by cold temperature. Eggs fail to hatch at 9°C and larvae fail to pupate at 15°C (O'Flynn, 1983).

The life cycle results obtained are similar to other studies (Table 3) indicating that *Chrysomya rufifacies* has a shorter life cycle than other calliphorids. Larval development time is variable and can be influenced by several factors such as temperature, humidity, breeding media and density of larvae.

Chrysomya rufifacies is unusual in that it produces monogenic offspring. Ullerich (1984) found that the sex determination in *C. rufifacies* is controlled by a non sex-linked dominant gene, named the female sex realiser (F). The female-producing females are heterozygous for this dominant allele, while male-producing females and males are homozygous for the recessive allele (f). The sex realiser is synthesized by the germ-line cells and is expressed during oogenesis.

The proportion of male-producing females to female-producing females in the wild population is not known, nor whether this proportion changes to take advantage of seasonal conditions. Further work is needed in this area.

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