FIELD & LABORATORY STUDIES ON POPULATION DYNAMICS AND DISPERSAL OF GRAIN WEEVILS (COLEOPTERA : CURCULIONIDAE)

by

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TABLE OF CONTENTS

SUMMARY

The grain weevils, *Sitophilus granarius* L. and *Sitophilus oryzae* L. first appeared in numbers sufficient to cause alarm to grain producers in South Australia in 1917. These species have continued to be major pests of stored grain throughout the State. The breeding and feeding activities of the adults and larvae result in the conversion of grains into husks, frass and broken pieces of endosperm,~~which are of no economic value to mankind.~~

Field experiments carried out to investigate the population dynamics and dispersal of *Sitophilus* spp under fluctuating weather conditions on the farms are discussed. These experiments confirmed that temperature and, to a lesser degree, grain moisture were major factors limiting the numbers of either species in small grain accumulations. The results suggested that there are two critical periods in the life-cycles of both species during which the weather influences population growth. The first critical period is in summer (December - February) when adults might be exposed to hot and arid conditions. Whereas summer temperatures of 40°C and above appeared to have no marked effect on the survivorship of *S.granarius* they caused annihilation of ~~small colonies of~~ *S.oryzae*. The second critical period is in winter (May - September) when oviposition and immature development might be greatly inhibited by subthreshold temperatures notwithstanding high survivorships in adult bettles. Egg production was highest in early summer when the oviposition rate of 30 eggs per female per fortnight was achieved. This compared with the oviposition rate of about 0.5 eggs per female per fortnight in winter. Developmental periods (egg - adult) ranged from about 30 days in December to 248 days in winter. Mortality of the immature stages was highest in mid-summer (January - February) and winter (June - August), with the highest tolls being observed in *S.oryzae*.

A colony of either species of *Sitophilus* comprises two classes of beetles namely, migrants and non-migrants. Migration in both density and temperature - dependent. However, the effect of these factors are not clearly marked until the colony population has grown to about 800 beetles/600 g wheat for *S.granarius* and 500 beetles/600 g wheat for *S.oryzae*. The latter species possesses a greater propensity to emigrate in response to density and other physical factors of the environment. About 70% of *S.granarius* were non-emigrants. These remained in the old habitats and died out when the food was completely exhausted. The corresponding proportion of non-emigrants of *S.oryzae* was about 40%. Olfactometer studies indicated that adults of both species could locate grains of about 14% moisture by means of their olfactory senses but failed to do so when dry wheat (11% m.c.) was offered as the food substrate.

Capacity for dispersal of either species in a standing crop of ripe wheat was measured in terms of metres travelled from a point of release per 2 day period. The maximum distances achieved over the entire period of observation of 21 days after release were 20 and 25 m for *S.oryzae* and *S.granarius*, respectively. This is equivalent to dispersal rates of 0.9 and 1.2 m/day. In laboratory and field tests *S.oryzae* did not disperse by flight. It is concluded that although *S.oryzae* possesses normal functional wings its mode of dispersal in nature, like that of its related unwinged *S.granarius*, is by walking.

16 samples (each sample consisting of 70 ears ≡ 100g shelled grain) taken at weekly intervals for a period of six weeks ~~Samples of grain taken at each sampling interval~~ in the dispersal experiment and incubated at 30°C and 70% R.H. did not yield any progeny; nor was there any evidence of damage on individual grains. It appears, therefore, that both species of *Sitophilus* have little, if any, ~~no~~ capacity to infest grain in the ears of a standing crop under the summer weather conditions experienced at harvest time in South Australia.

It is concluded that both species are not field pests of grain but only pests of stored grain. The continued existence of the problem of grain losses due to infestation by *Sitophilus* spp is ~~attributable~~ partially due ~~almost entirely~~ to poor farm hygiene. Existing farm hygienic methods aimed at keeping insect numbers at sub-economic damage levels are appraised.

Declaration

The work presented in this thesis is my own unless otherwise acknowledged, and has not, to my knowledge, been published previously or submitted to any University for the award of any degree or diploma

(Shadrack Sariri Mlambo)

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1. GENERAL INTRODUCTION

The grain weevil, *Sitophilus granarius* (L.) and the rice weevil, *Sitophilus oryzae* (L.) have been the subjects of many research programmes ever since their identification and recognition as pests of stored grain by Linnaeus in 1758. Although a lot of knowledge regarding the growth, development and control of weevil populations has accumulated as a result of those research programmes these two species remain the world's most widely distributed and destructive insects infesting stored grains and cereal products (Howe, 1952; Taylor, 1971). Both species are primary pests of stored grain (Cotton, 1950) and Davidson (1941), referring to damage to stored wheat in South Australia by *S.granarius* L., *S.oryzae* L., the beetle *Rhizopertha dominica* Fab. and the moth *Sitotroga cerellela.* Olive wrote: "The damage to stored grain by these species makes the material favourable food for a large number of secondary insects which are normally associated with crushed or ground cereal products".

The principal direct effects of attack by both the adult and the larvae of these weevils are loss in weight, reduced germination and changes resulting from spontaneous heating due to insect activities which may result in mould attack and sprouting. This is usually accompanied by loss of nutritive value and palatability of the grain. The United Nations Food and Agricultural Organisation, which carried out a survey in 1947, estimated annual cereal losses caused by insect infestations during storage at 8%. If grain losses incurred on the farms were included, total losses would amount to 10% of the world's annual cereal production (Munro, 1966).

Supposedly natives of the Orient or the Mediterranean sea region (Back and Cotton, 1926; Evans, 1979) the grain and rice weevils are now distributed all over the world (Cotton, 1950; Edward and Heath, 1964). *S.granarius* is principally a pest of temperate regions (Back and Cotton, 1926; Cotton, 1950; Surtees, 1963; Taylor, 1971; Champ and Dyte, 1976; Anon., 1978) but has often been recorded on grain imported into tropical countries (Back and Cotton 1926; Howe, 1953). It is commonly found infesting barley, wheat and other grains in the granary. *S.oryzae*, together with a closely related species *Sitophilus zeamais* Motsch, are commonly found on rice, maize, guinea-corn, wheat and other cereals throughout the temperate regions of the world (Hinds and Turner, 1911; Prevett, 1960; Kiritani, 1965; McFarlane, 1968; Champ and Dyte, 1976). The latter, formerly known as *S.oryzae* (large strain) but now identified as *S.zeamais* Motsch, (Kruschel, 1961; Halstead, 1962, 1964; Blickenstaff, 1968) is a well known flier and infests maize and other cereals both in the field and in storage (Hinds & Turner, 1911; Gurney, 1918; Birch, 1953; Kiritani, 1959; Giles and Ashman, 1971; Taylor, 1971). However, this species is not a candidate for my study and therefore apart from a brief mention under Dispersal, is not considered further in this thesis.

In Australia, since the early 1960s, efforts to protect stored grain and cereal products from insect damage have relied principally upon the application of pesticides used as contact insecticides, fumigants, fungicides and acaricides. These are applied in empty storage buildings and transport equipment for prophylaxis and directly on to grain or cereal products in bulk or bags for remedial measures. The basis for effective pest control by this technique is absolute efficacy of the chemical, air-tightness and sound design of storage buildings and containers, and the maintenance of a high standard of hygiene.

There are difficulties in the successful use of chemicals to prevent and treat grain infestations in the stores as well as in the field. The continuous application of contact chemicals results in the selection of resistant weevil strains (Champ & Cribb, 1965; Parkin, 1965; Dyte & Blackman, 1970; Monro, Upitis and Bond, 1972; Freeman, 1974; Levinson and Levinson, 1979,p.329). In fact "all important grain pests have now developed varying degrees of resistance, not only to malathion, but to all other pesticides that are fully acceptable internationally" (Champ, 1977 p.99). Other constraints to the use of pesticides include their ever increasing costs, shortages of supply, (especially in the developing countries), environmental pollution, and the dangers to non-target organisms.

Because of the increasing demand for cereal foodstuffs especially among the developing nations, and public concern over the hazards associated with the use of some of the most effective agricultural chemicals, a new urgency has been lent to the search for new and safer alternative pest control methods. Among such endeavours are research programmes involving irradiation of grain, sterile insect releases, inert atmospheres, refrigerated aeration, thermal disinfestation and ~~prevention~~ reduction of infestations by farm hygiene.

Large quantities of grain may be sterilized by irradiation with gamma rays (2 krad) from a source such as ^{60}Co or by electrons from an electron-accelerating machine (Cornwell & Morris, 1959; Cornwell & Bull, 1960; Brower, Hossain and Tilton, 1973). Although this technique has been successfully applied with large quantities of grain it has little scope for small grain producers because of the high expense and advanced technology involved.

The sterile-male release technique has been used to reduce insect infestations. The technique involves the intra-specific destruction of a natural population by means of induced sterility. This is achieved by artificially sterilizing wild males of that particular population by means of radiation sterility, chemosterilization, cytoplasmic incompatibility or hybrid sterility (Knipling, 1968; Weidhaas, 1968). Such sterilised males are then released into the natural population and allowed to compete with fertile males for mates. This disruption of the normal reproductive activity of the species acts as a check against population increase and may reduce it to sub-economic damage levels. However since reduction in population density by this technique is not permanent, further releases at appropriate times, are required. Knipling (1955, 1968) has discussed the requirements for the successful application of this technique, among them being a sound knowledge of the biology, ecology and population dynamics of the species concerned.

The advantages of this technique over chemical control is that it is species - specific, non-polluting and can be integrated with other techniques to control insect infestations. Such an integrated control programme has been applied with success in controlling *Dacus* spp (Steiner, *et al.* 1965; Steiner, *et al.* 1970; Economopoulos, *et al.*, 1977) and *Ceratitis* spp (Rhodes, *et al.* 1971). Lachance (1974, pp 56-57) has listed a number of harmful insects whose populations have been effectively reduced to sub-economic damage levels in small and medium-sized field tests in various parts of the world. The release of sterilised insects could be an effective method of suppressing and possibly eradicating injurious insect populations providing the insect species concerned can be easily mass-reared and released in sufficient numbers at the appropriate periods.

Literature on the prospects of controlling grain beetles by the use of this technique is lacking. Erdman (1974) suggested its exclusion from control efforts against flour beetles because of potential damage and sanitary problems likely to result from the presence of released adult beetles. Although promising results were achieved with the mill moth *Ephestia kuehniella*, Crook, *et al.* (1967) have concluded that the use of the sterile-male control method in stored products entomology is impracticable because of certain undesirable environmental and biological factors.

Biological control has also received some consideration. Where grain is to be stored for long periods predatory mites are thought to be effective in suppressing grain pest populations. These may be applied on their own or in combination with chemical techniques (Norris, 1958; Pulpan and Verner, 1965; Graham, 1970). However, biological control is generally thought unsuitable for combat~~t~~ing insect infestations in stored grain because the presence of large numbers of parasites is likely to cause insanitary conditions in stored grain products (Freeman, 1974; Bailey, 1975).

A new technique for controlling insect pests of stored grain has been published by Levinson and Levinson (1979). The method involves the integrated manipulation of the pests by mass-trapping them with sex and food attractants combined with a limited application of insecticidal fumigants. The technique has been shown to be both useful in early detection of an infestation as well as prevention of a population build-up. The method has achieved good results of reducing population densities of phycitid and gelechiid moths, dermestid and circulionid beetle pests of stored grain and stored cereal products to levels that do not cause economic damage.

The concept of aeration as a measure against grain infestations has been reviewed in detail by Muckle and Stirling (1971) and Elder (1975, pp. 381-386, 389-417). The technique involves passing cold outside air through a grain bulk thereby cooling the grain to below the threshold temperature for development of the larvae. Hot sun drying and ventilation have been used to disinfect grain by reducing the grain moisture content to levels which make the grain less vulnerable to attack by insects. Although these processes may not kill adult insects directly, they suppress reproductive capacities. New Paragraph

A technique related to the above but killing the insects by asphyxiation involves the use of controlled nitrogen and carbon dioxide atmospheres (Winterbottom, 1922; Hyde *et al.* 1973; Jay and Pearman, 1973; Banks, 1975; Bailey, 1975; Storey, 1975; Shejbal, 1976; Banks and Annis, 1977).

A number of studies have recently been reported on methods of disinfesting grain by applying heated air from a moving fluidized bed (Baeyens and Goossen, 1973; Dermott and Evans, 1978). They have indicated that hot-air thermal disinfestation does not impair grain quality and is efficient providing an accurately-controlled, fully automatic system is developed. Nelson (1973) has reviewed the use of microwave and other radio-frequency energies while Kirkpatrick, Brower and Tilton (1972) have compared the effects of microwave and infra-red radiation on *Sitophilus oryzae*. Boulanger, *et al.* (1971) have estimated the capital cost of a unit capable of treating 5 tonnes of grain per hour using microwave heating to be in excess of $US 100,000 and a similar high frequency dielectric heating system to be $US 40,000. Even if the margin between insect kill and grain damage turns out to be wide the immense capital and other scale-up problems associated with high technology heating systems will limit their use, especially among poorer nations of the world.

Farm hygiene, as a technique for preventing insect infestations, is as old as the practice of grain storage itself. The general principle underlining farm hygiene is the prevention of carry-overs of grain insects from season to season in header debris, in grain residues left in and around warehouses, in transport equipment, silos and other storage areas (Winterbottom, 1922; Birks and McAuliffe, 1973). Grain handling authorities in all Australian States and Departments of Agriculture in other parts of the world have laid down the basic cleaning methods which advocate the complete removal and incineration of all residues of grain, straw and dust before insects gain access and start to breed in them. These techniques involve the application of compressed air, water under pressure, vacuum cleaning and other appropriate measures. However, Sinclair and White (1979) who have been investigating the effectiveness of these techniques in disinfesting combine harvesters have concluded that farm hygiene, on its own, will not achieve complete eradication of grain beetles. This conclusion was based on trap records, which continued to show the presence of grain and flour beetles after the combine harvesters had been thoroughly cleaned using the above methods. They have indicated that the construction of the header currently in use in Australia is such that it is not feasible to rid the machine of every beetle or grain residue.

Many earlier workers have approached the problems of grain storage entomology with conscientious intentions of taking all aspects into account, but field ecology studies have, in general, been lacking or have been secondary to laboratory research (Munro, 1966; Graham, 1970). ~~As a result of the paucity of our knowledge of the population dynamics of the grain and rice weevils under variable farm~~

~~climatic conditions, every effective control measure found has been short lived.~~ The studies reported in this thesis were aimed at throwing some light on the important aspects of the ecology, including the dispersal behaviour, of *Sitophilus* spp. in the field and grain stores in South Australia.

In South Australia grain crops are grown at altitudes ranging from about 10 to 600 m above sea-level and stored on the farms mainly for stockfeed and seed while the bulk of it is transported directly from the field to the Bulk Handling Authorities which store it in country silos "en route" to export port terminal silos. Grain is chemically treated against insect pests and held at country silos for variable periods depending on the availability of storage facilities at the export terminal silos from where it is shipped overseas and to other Australian markets. Grain spillages are not uncommon in and around farm warehouses and in combine harvesters and if weevils gain access and start breeding in them they provide sources of infestation for new-crop grain.

Before commencing my experimental work I undertook a preliminary survey aimed at unveiling the frequency of occurrence of *Sitophilus* and other stored grain pest species on the farms throughout the State. The results showed that approximately 90% of the farms harboured grain insect infestations with *Ephestia, Tribolium* and *Sitophilus* spp being the most abundant and widely distributed. These findings are in agreement with those previously published by the State Department of Agriculture (Birks and McAuliffe, 1973).

South Australia has a temperate climate with cool-cold wet winters and hot dry summers. Mean monthly temperatures range from 6-28°C with the diel temperature ranging from 0-47°C with the corresponding relative humidities varying from 100-6%. Average annual rainfall figures for the grain belt range from 250 mm in the Riverland to 750 mm in the coastal regions. The 250 mm isohyet is a guide to the outer limit of economic cereal growing and storage belt. Grain is grown during the cold wet winter and harvested during the hot arid summer season.

For most of the winter months (June - August) temperatures lie below the lower developmental threshold of 11 and 15°C for *S.granarius* and *S.oryzae*, respectively (Eastham and McCully, 1943; Richards, 1947; Birch, 1953; Howe, 1965). In the summer season (December - February) supra-optimal developmental temperatures of 31°C and above (Richards, 1947; Birch, 1953; Howe, 1965) are quite common. Fletcher (1911) and Bailey (1975) have indicated that temperatures of 42°C are lethal to grain insect pests. Grain weevils continue to be one of the most abundant and widely distributed groups throughout the State, notwithstanding the above stated unfavourable climatic conditions.

An investigation of the population dynamics and the capacity for dispersal of these weevil species and the effects of seasonal changes coupled with highly fluctuating weather conditions was clearly worthwhile and offered an opportunity to make comparative studies of the field biology and movement activities of *S.granarius* (unwinged) and *S.oryzae* (fully winged). The knowledge so contributed could be used as a benchmark upon which to frame new and more effective methods of protecting grain from weevil damage in warehouses.

In view of the complex nature of these interrelated studies I have organised this thesis into six chapters as follows:

1. General ~~I~~introduction.
2. Field biological studies.
3. Colonisation processes and ~~M~~migration.
4. Dynamics of an endemic warehouse population of *S.oryzae* at Moorook.
5. Capacity for dispersal.
6. General ~~D~~discussion and ~~C~~conclusion.

2 FIELD BIOLOGICAL STUDIES

2.1 Introduction

Both species of *Sitophilus* have been studied extensively in the laboratory (in particular by Eastham and McCully (1943); Birch (1945, a-c, 1953); Eastham and Segrove (1947); Richards (1944, 1947); Howe & Hole (1968); Preve~~n~~tt (1960), and Evans (1977a-c, 1979). Eastham and McCully (1943) reported on the oviposition behaviour of *Sitophilus granarius* under controlled conditions, while the classical studies of Birch, (1945 a-c, 1953) reported on the biology of *S.oryzae* and the effect of environmental factors upon the species population dynamics under various combinations of constant temperatures and humidities in the laboratory. Richards (1947) has studied the biology of both species together under the same laboratory conditions as those used by Eastham and McCully and Birch. McLagan and Dunn (1935) investigated the effects of population density upon fecundity, utilization of food and the frequency of copulation for *S.oryzae*. Eastham and Segrove (1947) have reported the theoretical zero developmental temperature for *S.granarius* to be 11°C. More recently Evans (1977a,b,c, 1979) has studied acclimation, survivorship and productivity of both insect species at 15°C and 70% R.H.

Summarising the estimates of optimal and minimal conditions for population increase of various stored products insects, Howe (1965) has shown those for *S.granarius* to vary from 15-30°C with a minimum relative humidity of 50% (11.2% grain moisture) and those for *S.oryzae* to vary from 17-31°C with a minimum relative humidity of 60% (13% grain moisture). The corresponding optimal range for *S.oryzae* reported by Birch (1945 a-c) was 15.2-31°C and minimum grain moisture of 10.5%.

A lot of knowledge concerning the population dynamics of *Sitophilus* and their behaviour under laboratory conditions has been gained. Control measures have been developed on the basis of these studies and yet grain weevils continue to be the most widely distributed insect pests of stored grain. One of the difficulties is that we do not know how far we can apply the results of experiments conducted under artificial conditions of the laboratory to the much more variable and complex environmental situations encountered on the farms or storage sheds. Published laboratory studies, such as those cited above, do not make it possible to predict with any certainty what the survival and reproductive rates would be in small quantities of grain for they provide insufficient information on the effects of the wide temperature fluctuations (Section 1) around the theoretical lower developmental threshold for the cold months of May - October and for the supra-optimal temperatures experienced throughout South Australia in December, January and February. The only information concerning the survival and productivity of *S.oryzae* under field conditions was given by McFarlane (1968) in various parts of Kenya.

The object of the studies reported in this section was to investigate the survival and productivity of both species of *Sitophilus* under highly fluctuating seasonal weather conditions that occur in wheat spillages on South Australian farms - where the two species are occasionally found infesting the same grain in the same warehouse. The fact that they continue to be major problems of stored grain throughout the State notwithstanding the accumulated knowledge gained from laboratory studies made an investigation of their field ecology justifiable.

Since a lot is already known about their life-histories under laboratory conditions I felt that no useful purpose could be served by carrying out further biological studies of the two species in constant conditions of the laboratory. However I made preliminary laboratory observations on the reproductive capacity of my test weevils to ensure that these strains behaved in a manner similar to those used by earlier workers, and to gain experience in handling and understanding them. The work on the biological studies has been organised as follows:

2.2 Materials and Methods

- 2.2.1 Description of experimental sites
- 2.2.2 Experimental medium
- 2.2.3 Insect stock cultures
- 2.2.4 Experimental cultures

2.3 Results and Discussion

- 2.3.1 Survivorship of the parental cohorts at each site per fortnight during each season of the year
- 2.3.2 Oviposition rates per fortnight at each site
- 2.3.3 Developmental periods and mortality of the immature stages at each site.

2.4 Summary

2.2 Materials and Methods

2.2.1 Description of experimental sites

Three sites were chosen to represent dry inlands (Moorook) (40 m), highlands with moderate rainfall (Palmer) (400 m) and comparatively damper coastal-lands (Adelaide) (50 m); all of which are situated within the cereal producing and storage-belt of South Australia. Infestations of grain by *Sitophilus* are not uncommon at all three sites.

Detailed information concerning the temperature and humidity data for the three sites are presented in Appendix Table 2.1, from where it can be seen that mean fortnightly temperatures, one of the most critical parameters for the survival and reproductive capacities of both species, fluctuate around the theoretical lower developmental limit for half the year (May - October). Published laboratory studies, such as those cited above, would give unreliable predictions of the survival and reproductive rates of *Sitophilus* spp under environmental conditions of these experimental sites. In large silos or any other large bulks of stored grain diel temperature fluctuations are negligible except near the surface, but in small grain accumulations typified by spillages on the farms, the diel temperature varies with that of the surrounding environment, but this would depend on the size + location of the spillage.

2.2.2 Experimental Medium

Olympic *8156 - a soft wheat variety produced by the Waite Agricultural Research Institute, and shown to be a good supportive medium for population growth of *Sitophilus* spp (Evans, 1977), was used throughout this project. Preliminary observations had shown a clear preference of *Sitophilus* for this variety compared with other varieties also locally produced.

The selected Olympic wheat was first sieved (sieve size 4 mesh to the cm) to remove grain dust, tiny grains and broken kernels since both species are primary colonists and will not normally oviposit in fragmented grain. The experimental grain was then sterilised at 75°C for two hours in the oven. The water content of the cooled grain was then determined and adjusted to bring it to 14% (= 70% R.H.) using the technique described by Richards (1947). The grain to be used for biological studies in the field was sealed in galvanised iron bins and kept at each experimental site for six weeks to allow it to equilibrate to site environmental conditions before beginning any experiment. For constant condition work appropriate relative humidities were achieved by the methods of Solomon (1951) and Anon. (1960).

2.2.3 Weevil stock cultures

Since the major objective of this ecological study was to compare the overall performance, with respect to survivorship, productivity and behaviour of small populations of the two species of *Sitophilus* under identical conditions, the test insects had to be of the same age with a comparable rearing background.

Two lots of 500 g of conditioned Olympic wheat were infested with 1000 adults of either *S.granarius* or *S.oryzae* originally collected from infested grain on the same farms where the studies were carried out. These were allowed to oviposit in grain contained in aerated jars at 29°C and 70% R.H. for 48 hours. The batches were then sieved off and eggs and the resulting larvae were incubated at 29°C and 70% R.H. A batch of 500 adult progeny of either species was used to inoculate further cultures and I expected that the 4th generation derived from such serial inoculations and needed for commencing experimental cultures would exhibit reduced genetic variability, an essential factor for qualitative comparative studies.

2.2.4 Experimental cultures

The experimental cultures were started in November 1977. Eight replicates of 100 g wheat equilibrated with the conditions of the sites were each inoculated with 15 ♂ + 15 ♀ beetles 1-2 days old. At that age they would not yet have commenced oviposition; based on a pre-oviposition period of 2 day for *S.oryzae* and 2-3 days for *S.granarius* at 25°C and 70% R.H. observed by Birch (1945b) and Eastham and McCully (1943), respectively. The pre-oviposition period at the site would have been at least 5 days. The sexing of test cohorts was achieved by means of Halstead's (1963) technique, and confirmed by the presence or absence of the aedeagus (male) through dissection of dead test beetles. The 8 cultures of either species were contained in polystyrene jars, 10 cm diameter and 12 cm deep and covered with ventilated lids. These, together with a thermogyrograph, were placed in an aluminium fly-wire cage to prevent intrusion by mice and placed inside the sheds. The setting up of experimental cultures was completed within two days; the wide distance between sites coupled with the amount of work involved prevented its completion within the same day. Experimental cultures for each season were started with new batches of test cohorts reared from the same parental stock under the same conditions as for previous test cohorts.

At two-weekly intervals mortality and sex of dead parents were recorded, at which times the surviving parents were transferred to fresh 100 g lots of equilibrated wheat. Estimates of eggs laid within each fortnight were made by staining infested wheat samples with acid fuschin (Frankenfeld, 1948) and microscopically locating the gelatinous egg plugs on the seed coat. At every observation two replicates of the wheat infested by either species were taken from the site and reared at 29°C + 70% R.H. as a check on the mortality of the immature stages in the 6 replicates left to develop to emergence without interruptions at the site. The water content of the experimental wheat was determined (Marconi moisture meter) from samples taken at each inspection interval. This gave a more accurate measure of the fluctuation pattern of the moisture content of experimental grain as this is known to lag behind that of the relative humidity of the surrounding air recorded by the thermohygrograph.

2.3 Results and Discussions

2.3.1 Longevity of Adults

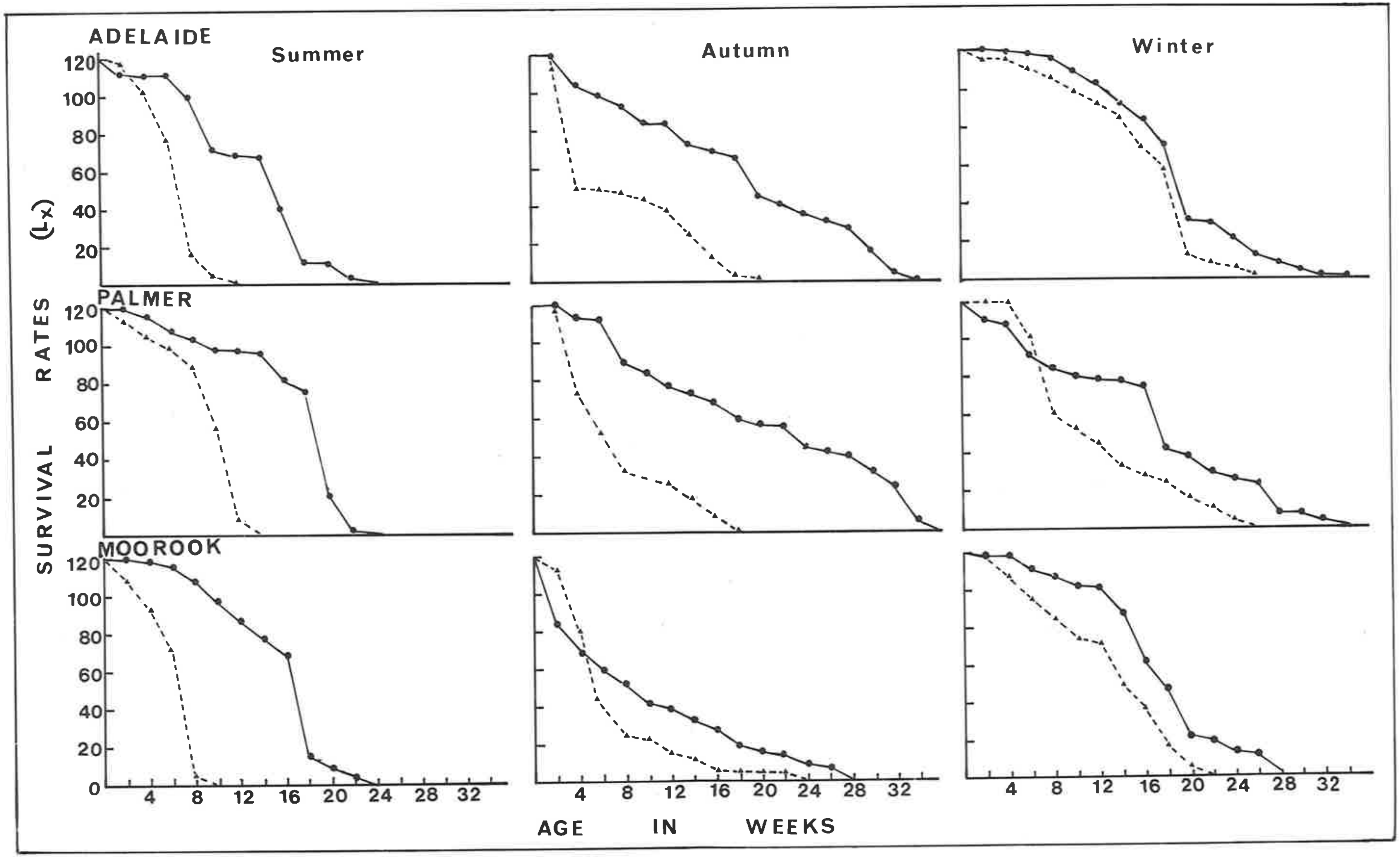
Mean longevities of the sexes were about the same for either species at all sites. Similar findings have been reported by Richards (1947), Birch (1953) and McFarlance (1968). Although survivorship schedules of both sexes were recorded the results reported below concern females only, since males do not contribute directly towards production of a new generation after mating has occurred. In fact, after a single mating, a female may continue ovipositing until death.

The results of the survival rates are shown graphically in Figure 2.5. The temperature and grain moisture data have been recorded in appendix Table 2.1. ~~Significant~~ Considerable mortality occurred

Figure 2.5: Generalised comparative survivorship rates (Lx) for ovipositing female beetles of *S.granarius* and *S.oryzae* in 100g lots of wheat under ambient conditions in farm storages ~~under field environmental conditions~~ at Adelaide, Palmer and Moorook.

●——● : *S. granarius*

▲·····▲ : *S. oryzae*


ADELAIDE
Summer
Autumn
Winter
PALMER
MOOROOK
120
100
80
60
40
20
0
(Lx)
SURVIVAL RATES
4
8
12
16
20
24
28
32
AGE IN WEEKS

in *S.oryzae* within the first fortnight of life and this sharply increased to exceed 50% during the 2nd and 4th fortnights. This coincided with lethal temperatures (Bailey, 1975) of 42 and 43°C and corresponding low moisture levels recorded at all the sites during the month of December (Appendix Table 2.1). *S.oryzae* adults had virtually been annihilated by the end of the 5th fortnight. *S.granarius* on the other hand, showed itself to be more resistant to the observed adverse environmental conditions. This susceptibility of *S.oryzae* to high temperatures and low moisture has also been observed by Segrove (1951) who also reported that at 9.9% moisture mortality of *S.oryzae* is high. The new experimental batches of *S.oryzae* exposed to site conditions in March (end of summer) were partially destroyed as a result of adverse environmental conditions experienced shortly after the experiment commenced but survivors showed greater longevities with successively decreasing temperatures in autumn and winter.

The mean longevities of both species under fluctuating environmental conditions of each site are summarized in Table 2.2. Clearly my results indicate a tendency for *S.oryzae* to live longer in cold weather than in autumn and hot arid summer weather. There were no significant differences in the survival rates of *S.granarius* between the different seasons. The mean longevities for *S.oryzae* are to be contrasted with those of other workers based mainly on controlled temperature and humidity conditions. These are 17 weeks at 29.1°C (Birch, 1953); 14 weeks on rice at a mean laboratory temperature of 27°C (Preve~~n~~tt, 1960) and 9 weeks at 25.5°C (McFarlane, 1968). The latter found no significant difference between his control and field cultures in Kenya. More recently Evans (1977) has found a mean longevity of 51 weeks for

S.oryzae at 15°C and 70% R.H. Mean longevitics of *S.granarius* were found to be 39 weeks at 20°C and 70% R.H. (Eastham and McCully, 1943), 25 weeks at 25°C and 70% R.H. (Richards, 1947) and 76 weeks at 15°C and 70% R.H. (Howe & Hole, 1968; Evans, 1977).

Table 2.2: Mean lengths of life (in weeks) of ovipositing mothers reared at 29°C and 70% R.H. and transferred as 1-2 day-old adults to fluctuating weather conditions of the site.

Site and species	Season and mean longevity in weeks		
	Summer	Autumn	Winter
<u>Adelaide</u>			
S.granarius	16	19	19
S.oryzae	7	8	17
<u>Palmer</u>			
S.granarius	17	16	15
S.oryzae	10	9	14
<u>Moorook</u>			
S.granarius	16	10	17
S.oryzae	7	8	14

These results accord with those reported by Gonen (1977). The latter showed that *S.granarius* has a superior ability to acclimate (i.e. adjust phenotypically to the altered temperature) to variable temperatures than *S.oryzae*. Hence it survived much longer than *S.oryzae* in summer. However, the latter also survived at temperatures well above that considered to be lethal by Birth (1945a), including the 40°C reported to be the thermal death point (Herford, 1948). A similar trend has also been reported by Evans (1977c) with respect to subthreshold temperature.

2.3.2 Age - Specific Fecundity

The fortnightly rates of oviposition during the life of each species at each site are shown in Appendix Table 2.1, together with data on the corresponding temperature and moisture levels.

In both species reproduction began within the 1st fortnight, though with greater intensity for *S.oryzae* than for *S.granarius* during the summer and autumn seasons. The rate of oviposition reached its peak during the 3rd fortnight in summer but the trend was rather different between the sites in autumn. The peaks came earlier in autumn (Figure 2.6) than in summer, probably because the environmental conditions were nearly optimal at the onset of the second batch of experimental cultures. Oviposition rates by the few females which survived beyond the end of each season are not included in Figure 2.6 but have been accounted for in the fecundity Table 2.3. In winter the order of commencement of reproduction was reversed with *S.granarius* beginning oviposition in the 2nd fortnight of life at Adelaide and Moorook and in the 3rd fortnight at Palmer. *S.oryzae*, on the other hand, commenced oviposition, though sporadically, during the 3rd fortnight at Moorook, 4th at Adelaide and 5th at Palmer. The peak was reached simultaneously at all sites in the 7th fortnight. Thereafter the oviposition rates gradually decreased. As was the case in the previous summer *S.oryzae* died out in December, 1978 while *S.granarius* survived until February 1979. Although survivorships of adult beetles remained high at the end of the cold season in October the ageing factor militated against any increase in the oviposition rates which steadily declined until completion in mid-summer. The mean numbers of eggs laid per female during her life span are shown in Table 2.3.

Figure 2.6 : Comparative oviposition rates (mean number of eggs/♀/fortnight) for *S.granarius* (solid line) and *S.oryzae* (broken line) in 100g lots of wheat under ambient ~~under field environmental~~ conditions at Adelaide, Palmer and Moorook.

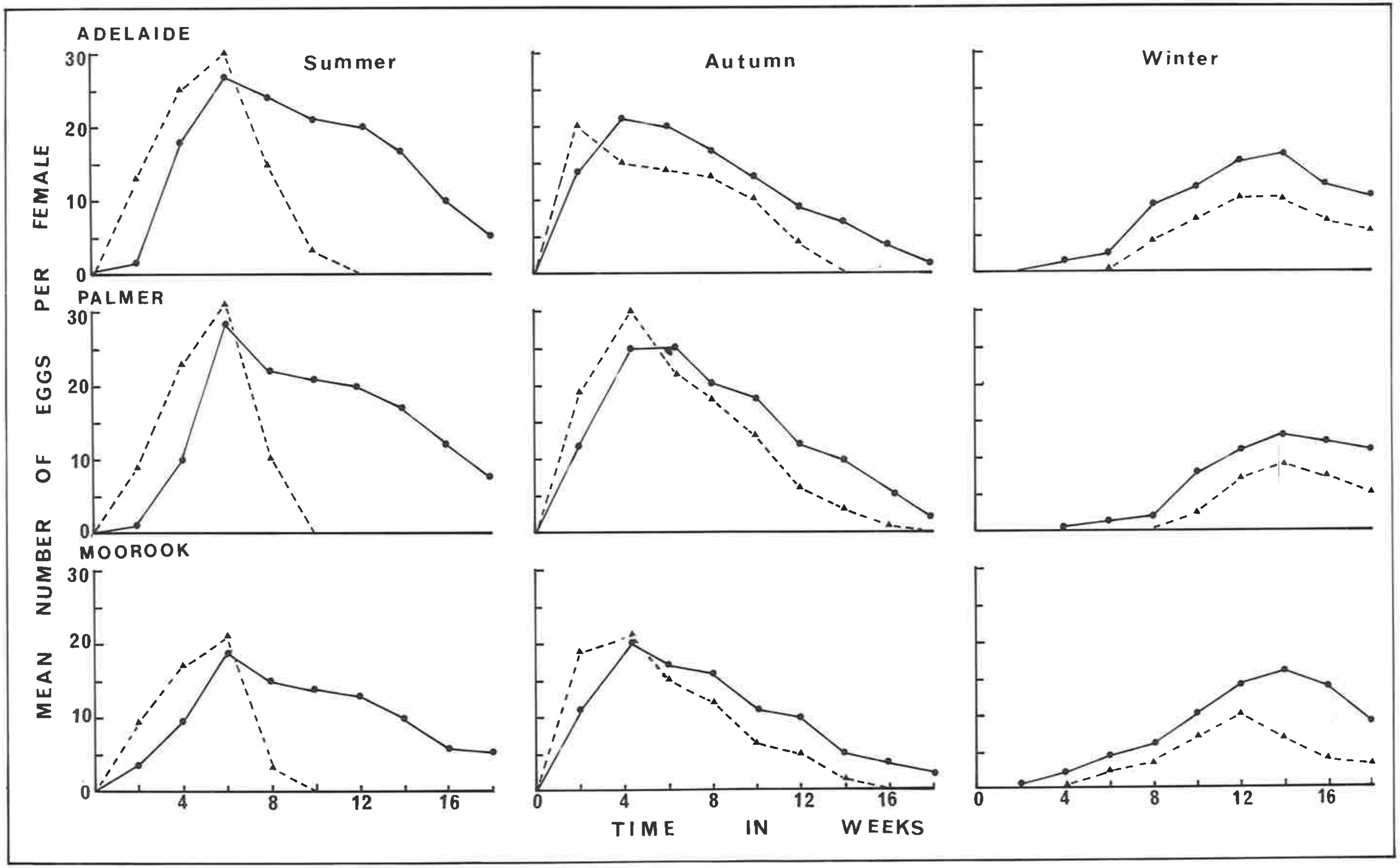

ADELAIDE
PALMER
MOOROOK
Summer
Autumn
Winter
MEAN NUMBER OF EGGS PER FEMALE
30
20
10
0
4
8
12
16
TIME IN WEEKS

Table 2.3: Fecundities of *S.granarius* and *S.oryzae* at each site expressed as the average number of eggs produced per female during her life span.

Site and species	Mean number of eggs produced per female/life span. (Eggs ± S.E.) n = 8		
	Summer	Autumn	Winter
Adelaide			
S.granarius	155.2±2.7	114.5±2.1	99.4±1.5
S.oryzae	108.1±2.1	92.6±2.3	51.4±1.0
Palmer			
S.granarius	177.7±2.2	132.8±2.7	110.7±1.2
S.oryzae	77.7±4.9	110.8±3.4	42.0±0.88
Moorook			
S.granarius	108.5±1.7	103.5±2.1	96.0±1.6
S.oryzae	51.0±0.8	76.3±2.4	45.4±0.8

The observed oviposition rates and fecundities indicate that although *S.granarius* has been shown to be less fecund than *S.oryzae* under optimal conditions (Richards, 1947; Evans, 1977a,b), under the widely fluctuating weather conditions experienced in this study, its population would be expected to grow at a faster rate than that of the latter by virtue of its higher tolerance to these unsuitable weather conditions. Laboratory data on these species by previous workers are not comparable since environmental conditions were different. However, these were as follows: 344 eggs/♀ lifespan at 25.5°C and 70% R.H. (Birch, 1953), 68 eggs for *S.oryzae* at an average temperture of 27°C (Preve~~n~~tt, 1960). Richards (1947) has reported a mean fecundity of 191.5 eggs per *S.granarius* female at 25°C and 70% R.H. Evans (1977a,b) reported lower values for both species reared at 27°C and 70% R.H. and held at 15°C and 70% R.H.

Table 2.4: Mortality of the immature stages of *S.granarius* and *S.oryzae* under site conditions compared with those transferred as eggs and reared at 29°C and 70% R.H. (C.C.). (Mean No. ± S.E./♀/lifespan).

Site and species	Season	E/♀/lifespan	Progeny/♀/lifespan C.C.	Progeny/♀/lifespan Site	% Mortality C.C.	% Mortality Site
Adelaide	Summer					
S.granarius		155.2	111.8 ± 2.4	98.3 ± 2.1	28	~~12~~ 63
S.oryzae		108.1	55.7 ± 4.2	35.2 ± 3.7	49	~~37~~ 33
Palmer	"					
S.granarius		177.7	118.4 ± 2.1	105.1 ± 2.3	33	~~11~~ 59
S.oryzae		77.7	54.9 ± 4.1	31.6 ± 1.8	29	~~42~~ 41
Moorook	"					
S.granarius		108.5	74.4 ± 1.8	54.4 ± 4.1	31	~~27~~ 50
S.oryzae		51.0	37.5 ± 1.5	17.0 ± 1.9	27	~~55~~ 33
Adelaide	Autumn					
S.granarius		114.5	79.4 ± 2.1	61.1 ± 2.0	31	~~23~~ 53
S.oryzae		92.6	55.1 ± 1.3	46.5 ± 1.6	50	~~26~~ 50
Palmer	"					
S.granarius		132.8	106.0 ± 2.4	84.3 ± 2.6	20	~~20~~ 63
S.oryzae		110.8	59.5 ± 2.2	34.5 ± 2.4	47	~~42~~ 31
Moorook	"					
S.granarius		103.5	68.7 ± 2.0	46.3 ± 2.2	34	~~33~~ 45
S.oryzae		76.3	40.0 ± 2.2	16.9 ± 1.7	48	~~58~~ 22
Adelaide	Winter					
S.granarius		99.4	55.1 ± 1.8	33.9 ± 1.1	44	~~38~~ 34
S.oryzae		51.1	19.5 ± 0.4	9.7 ± 0.6	62	~~50~~ 19
Palmer	"					
S.granarius		110.7	54.4 ± 1.5	37.5 ± 1.5	49	~~31~~ 34
S.oryzae		42.0	18.5 ± 0.5	7.4 ± 0.6	56	~~60~~ 18
Moorook	"					
S.granarius		96.0	57.4 ± 1.4	41.4 ± 1.2	40	~~38~~ 43
S.oryzae		45.4	18.8 ± 0.7	7.6 ± 0.3	58	~~61~~ 17

2.3.3 Developmental durations and Mortality of the Immature stages

Once the adults had begun emerging, the experimental cultures were brought to Adelaide where progeny could be harvested at short intervals before the offspring could begin ovipositing.

The precise time required to develop from egg to adult could not be estimated. The cultures were commenced with young adults, not with eggs of known age, so the date on which the first eggs were laid could have been anywhere within that 14 day period. Similarly, the day of first emergence at the site could have been anywhere within the fortnight since the previous observation. In general, for any given combinations of temperatures and moisture levels the first emergence could have been earlier where the density of the immature stages was high since these create a microclimate in their habitat which acts as a buffer against adverse weather conditions of the surrounding environment (Howe, 1953).

The times observed for each species to develop from egg to emergence of progeny from the grains under field conditions are presented graphically in Figure 2.7. The immature survival rates at each site, together with those transferred as eggs and reared under optimal conditions (check) are shown in Figure 2.8. Table 2.4 has been included to show the proportion of eggs which failed to complete development (egg-emergence) under site and standard conditions.

In Table 2.4 I have included the mortality values for the replicate egg cultures which were transferred from the sites and reared at 29°C and 70% R.H. as a check on egg viability against

Figure 2.7: Observed mean developmental durations for *S.granarius* (solid line) and *S.oryzae* (broken line) under fluctuating environmental conditions of the site. Each period was measured from the middle of the oviposition period to the middle of the emergence period.

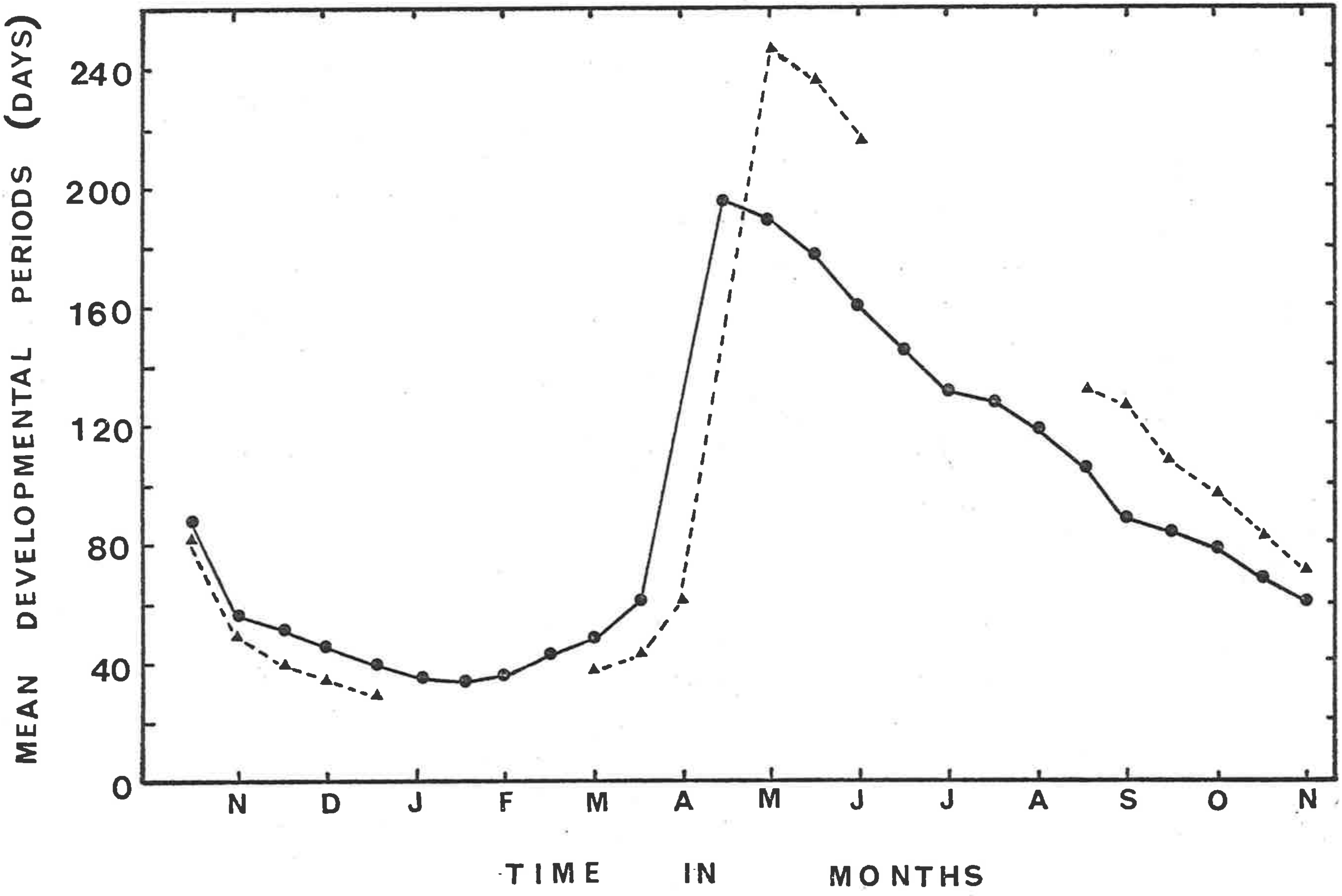
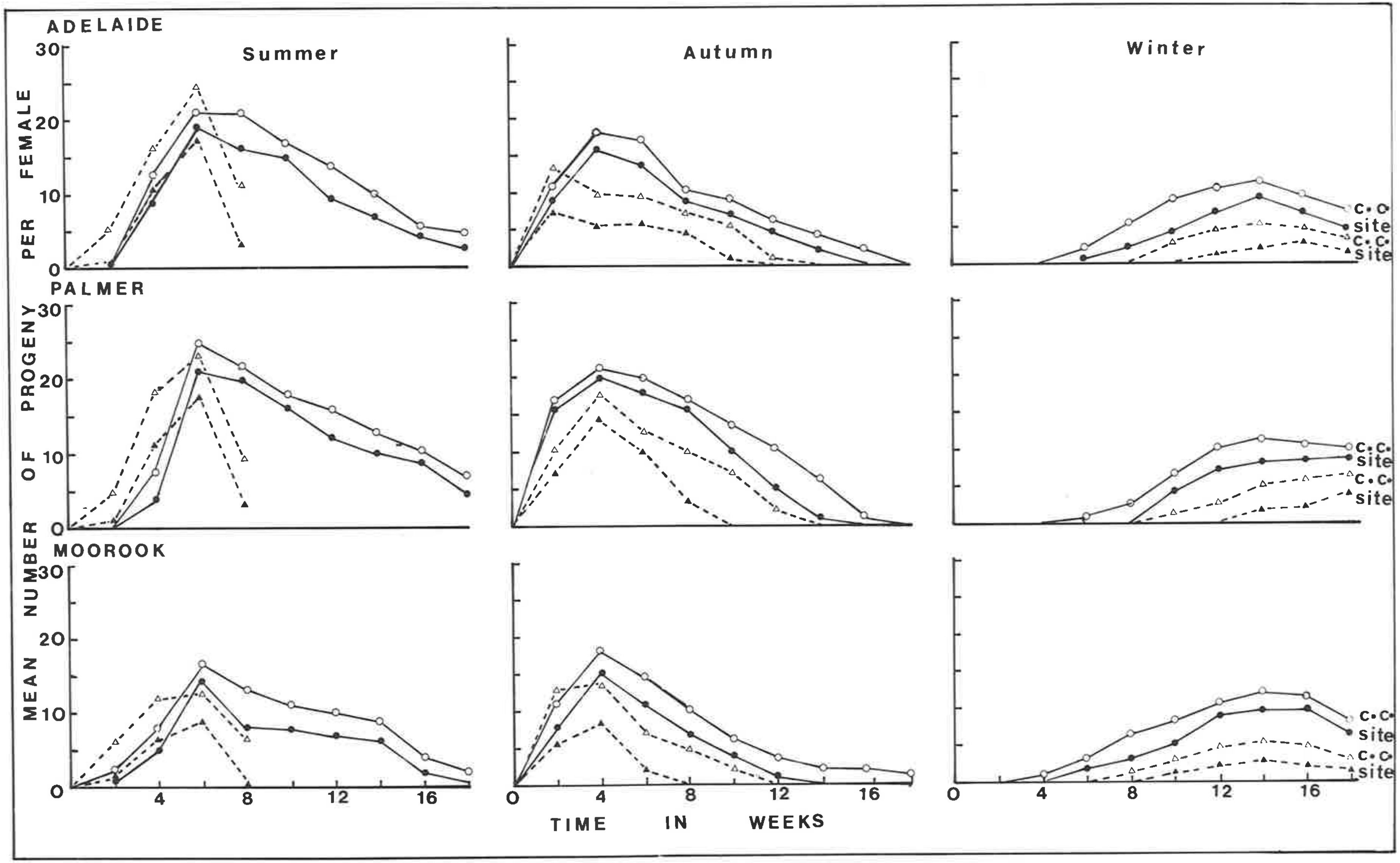

MEAN DEVELOPMENTAL PERIODS (DAYS)
0
40
80
120
160
200
240
N
D
J
F
M
A
M
J
J
A
S
O
N
TIME IN MONTHS

Figure 2.8: Immature survival - Generalised mean number of progeny/♀/fortnight for *S.granarius* (solid line) and *S.oryzae* (broken line) under field conditions at Adelaide, Palmer and Moorook compared with those transferred from each site and reared at 29°C and 70% R.H. (c.c).


ADELAIDE
Summer
Autumn
Winter
PALMER
MOOROOK
MEAN NUMBER OF PROGENY PER FEMALE
0
10
20
30
0
4
8
12
16
TIME IN WEEKS
c.c.
site
c.c.
site

those replicates left to develop to emergence under the fluctuating environmental conditions of the site. The shortest developmental period of 30 days for *S.oryzae* was recorded in summer (December) and the longest duration of 248 days recorded for the eggs laid in May where emergence was delayed until early summer. These compare with 64 days at 22.5°C (20.5-26.3), 177 days at 13.5°C (5.5-23) and 272 days at 11.9°C (5-20) recorded by McFarlane (1968) in various parts of Kenya, and 68 days at an average ambient temperature of 27°C recorded by Preve~~n~~tt (1960). Other workers, notably Birch (1945a), reported about 28 days at 29.1°C and 70% R.H. and 216 days at 15.2°C and 70% R.H. and Evans (1977a) recorded about 195 days at 15°C and 70% R.H.

The corresponding periods for *S.granarius* were 35 days recorded in January and 185 days for the May eggs where emergence was recorded in November. These results compare with 32 days at 30°C and 70% R.H., 44 days at 25°C and 70% R.H., 59 days at 22.5°C and 70% R.H. and 148 days at 15°C and 70% recorded by Eastham and Segrove (1947). Richards (1947) reported 45 days at 25°C and 70% R.H. and more recently Evans (1977b) has reported 158 days at 15°C and 70% R.H.

S.oryzae has shorter developmental periods than *S.granarius* at optimal ranges of temperature and moisture but at subthreshold temperatures (when in this case moisture remained optimal) these developmental periods become greatly lengthened, in fact longer than those of *S.granarius* (Figure 2.7). The immature stages of *S.oryzae* are susceptible to high (summer) and low (winter) temperatures and no development occurs at the extreme temperatures experienced during those seasons (Figures 2.7 and 2.8). Because

S.granarius has a lower developmental threshold, 11°C compared with 15°C for *S.oryzae*, it was able to complete development in winter when temperatures as low as 2 or 0°C were occasionally experienced. Howe (1963) has suggested that exposure of insects to subthreshold temperatures has a cumulative effect, but short exposure to favourable temperatures removes the developmental blockage, and regular diurnal exposures to above subthreshold temperature enable development to proceed. This could be the explanation for the progeny observed during the cold months (May - September) when mean temperatures of 7 -15°C were recorded.

It has been shown (Evans, 1977a,b) that *S.granarius* is slower to start reproduction and is less fecund than *S.oryzae* under identical conditions (15°C and 70% R.H.) but its immature stages survive better than those of the latter. He recorded a survival rate of only 16.5% for *S.oryzae* compared with 41% for *S.granarius*. My results are in general accord with those findings except that at supra-optimal and subthreshold temperatures and low humidities *S.granarius* behaves in a way that is more likely to promote survival and reproduction than does *S.oryzae*.

2.4 Summary

Survivorship and reproductive capacities of both species vary according to temperature. The meteorological data recorded at all sites were not significantly different and consequently the observed trends with respect to the survivorships and reproductive performances were nearly similar. As could be expected *S.granarius* showed superior performance with respect to parental cohort survivorship and all aspects of reproduction. This investigation has demonstrated that the climate of South Australia is such that *S.granarius* can usually survive and maintain its population in small grain accumulations. *S.oryzae* could face extinction as temperatures of 42°C and above, with corresponding low moisture contents, are likely to kill all stages. However, the survival and reproductive potential of this species will improve with an increase in the size of the grain accumulation and insect density (Section 3.3), notwithstanding the adverse conditions discussed above.

In experiments (such as those described above) where the components of the environment were not controlled it would be difficult to single out any one parameter or a combination of them as having exerted more influence on the observed reproductive capacities. However, it seems likely that temperature had an overwhelming effect on the various phases of the beetles lives. In summer, reproduction in *S.oryzae* ceased abruptly after only 8 - 10 weeks of life when all the adults died. This coincided with the occurrence of very high temperatures. In winter survivorship of parental cohorts of both species was high but reproductive capacities were low and immature development retarded or incomplete as temperatures fell to subthreshold levels.

3 COLONISATION AND BEHAVIOUR OF ADULT BEETLES

3.1 Introduction

The establishment and rates of growth of small populations of weevils in small accumulations of grain on farms may be of great economic importance. When attempting to assess the importance of such infestation processes from a behavioural point of view, perhaps two basic questions ought to be asked:

i) What makes *S.granarius* and *S.oryzae* leave the habitat they are breeding in?

ii) How can individual *S.granarius* or *S.oryzae* find a new source of food for itself and for the next generation?

Working under artifically controlled environmental conditions Birch (1946); Howe (1951) and Surtees (1963a & d, 1964,a,b,c & d) have demonstrated that movements of these species within bulks of grain are influenced by temperature, humidity, insect density, quality of food, sex of the beetles and whether they have mated or are unmated. Whereas the information derived from such investigations may have some bearing on the answer to question i) it does not throw any light at all on question ii). Yet the latter question involves an essential aspect of the weevil's life and our knowledge of it is fundamental to the understanding of the inception and development of infestations in nature. Such knowledge is useful not only for the prediction of infestations of accumulations of grain but, more importantly, for the prevention of the colonisation itself.

The primary object of the studies described in this section was to determine the ecological significance of crowding upon emigration of the grain and rice weevils breeding uninterruptedly in "natural habitats". A further objective was to investigate the role of food odours in enabling *Sitophilus* spp to locate sources of food.

In carrying out the work to be described below I was guided by the following general hypotheses:

a) *S.granarius* and *S.oryzae* are primary colonists. Adults of both species will multiply wherever undamaged grain accumulates.

b) A colony does not comprise distinct groups of emigrants and non-emigrants. Adults of both species exhibit tendencies to emigrate in response to density and temperature.

c) Adults of both species locate their food by means of their olfactory senses.

This section has been organised in three sub-sections as a convenient way of showing the relationship between them. These are as follows:

3.2 Progress in population growth to emigrant status
3.3 Further studies on migratory behaviour
3.4 Observations on food searching ability
3.5 Summary

3.2 Progress in population growth to emigrant status

3.2.1 Introduction

The factors responsible, at different insect densities, for the successful establishment of an infestation and the reduction in reproductive rates, from very high values during the initial build-up in numbers to much lower values when the population becomes dense, have been investigated under controlled conditions and analysed by McLagan (1932) and McLagan and Dunn (1935). The former has also postulated that the fundamental factor underlying the urge to depart from the habitat is the "psychological effect" of excessive contact stimulation due to crowded conditions of existence. This factor was thought to come into operation long before there is any real or apparent shortage of food.

The study reported in this subsection investigated hypotheses (a) and (b) already stated above. Specifically, it tests qualitatively the predictions that both species of *Sitophilus* can establish colonies wherever sound grain exists. Such colonies do not consist of emigrants and non-emigrants but that adult beetles will emigrate in response to density and temperature.

3.2.2 Materials and Methods

The experimental habitats consisted of 600 g equilibrated wheat (See Section 2.3) held in inverted 1 kg plastic jars whose wider, open ends were glued on to the bottoms of 5 kg clear modular canisters (Plate 3.21). The mouth of each jar was covered with gauze whose aperture was big enough to allow free passage of the largest sized beetle. A band of "Fluon"* ran across the outer wall of the jar to prevent emigrants climbing back into their old habitat. The inner wall of the canister was also banded with fluon to prevent the catch from escaping from the collection chamber (Radinovisky and Krantz, 1962). This apparatus acted as a One-way trap, the idea of which was based on that of Prus (1963).

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* "Fluon" is the common name of Polytetrafluoroethylene Dispersion, Grade G.P.1 supplied by Imperial Chemical Industries Ltd., Herts. U.K.

Plate 3.21: The One-Way trap used to study the emigration behaviour of grain weevils.

Opaque plastic container (inside) held experimental cultures.

Gauze for aeration and free passage of weevils.

Clear Modular Canister (outside) - collection chamber for emigrants.

Band of "Fluon" (white) - to prevent escape of emigrants.

At time "Zero" the lots of wheat were inoculated with 1-3 day-old weevils of either species (cohorts obtained by the method described in Section 2.3). The design was as follows:

Experimental Culture	Density equivalence (Food ratio)
15♂ + 15♀ weevils/600 g wheat x 10 replicates	667 grains/beetle
30♂ + 30♀ -ditto-	334 " "
60♂ + 60♀ -ditto-	167 " "
120♂ + 120♀ -ditto-	83 " "

Thermocouples were built into 3 "permanent"* replicates of each treatment of both species to monitor temperature changes which normally result from rapid reproductive and feeding activities. Increase in temperature is thought to trigger departure of most adult insects (Howe, 1951). The positions of the experimental cultures were randomised. The plastic culture containers remained covered for 7 days to allow the test insects to establish themselves in the new habitats. Then the covers were removed. The beetles could move to the surface of the wheat, climb up the inner walls of the jar and reach the top by passing through the gauze apertures. Beetles could walk about on the top and either re-enter and return to their habitat or depart into the new environment by walking down the outer walls to reach the floor of the collection chamber.

In this experiment an emigrant has been defined as that beetle which made a no-return trip and was subsequently trapped and recovered from the collection chambers. Those wanderers who made exit trips but returned, together with those which stayed notwithstanding the mounting population density and the deteriorating conditions of the habitat have been categorised as non-emigrants.

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* These were habitats which were not to be demolished until the insect populations breeding in them had all died out.

At two-weekly intervals the emigrants were collected and their numbers recorded according to sex. Extreme care was exercised throughout the experiment to avoid mechanical disturbance as this is known to cause mass exodus of beetles (Dendy and Elkington, 1920).

At eight-weekly intervals one replicate per treatment group was demolished to estimate the total population size in order to relate it to the observed emigration patterns.

3.2.3 Results and Discussion

The investigation was commenced in December 1977 and concluded in February 1979 at which time all beetle populations had become extinct. The study differed from earlier studies, based mainly on *Sitophilus granarius* and *Tribolium* spp (Surtees, 1963a; 1964a-d; Ziegler, 1976, 1977) in that in my experiments emigration was observed over the entire life of the colonies of either species of *Sitophilus*.

Population Growth Processes:

The population growth rates and emigration patterns are shown graphically in Figure 3.3a-d. The solid line curves represent the numbers of non-emigrants found in the habitats at demolition intervals. Each point on the emigration curves (broken line graphs) represents the cumulative number of beetles collected from the trap for that corresponding habitat at fortnightly intervals up to demolition time. Colony size for any particular density at any given time may be found by summation of emigrant and non-emigrant numbers at corresponding times.

There were ~~significant~~ marked differences in colony growth rates between the two species. All the densities of *S.oryzae*, except the lowest

(30 beetles per 600 g wheat) commenced reproduction almost immediately after artificial infestation. They reached high peaks of 7,000 weevils per colony and above during the 16th week; thereafter the rates gradually declined. *S.granarius*, on the other hand, was less successful in getting established in the new wheat cultures. Only the highest density (240 beetles/600 g wheat) behaved in a manner similar to that of the intermediate densities of *S.oryzae*. The higher turnover of new generation beetles of *S.oryzae* was to be expected since this species has a higher finite rate of increase (λ) of 25 (per female/4 weeks) compared with that of 15 for *S.granarius* based on optimal controlled conditions (Howe, 1965). What came as a surprise was the failure of the intermediate densities of *S.granarius* to establish themselves and commence reproduction as their counterparts *S.oryzae* had done. In fact there was no significant difference between them and the lowest density of *S.oryzae* which never effectively took off from the starting positions. The lowest density (30 beetles/600 g wheat) of *S.granarius* produced very few beetles and there was no emigration. A possible explanation may have been their failure to exert moderating influences over the adverse factors of the surrounding environment. High supra-optimal temperatures identical with those of the surrounding environment were recorded in those cultures during the months of December - February (not shown in Figure 3.4). These caused a drastic fall in the moisture content of the grain (Figure 3.3a-c), making it too dry for weevils to successfully establish feeding and oviposition sites. The observed moisture levels of 8.0 - 9.5% fall far below the lower threshold levels of 11.2% (= 50% R.H.) and 13.2% (= 60% R.H.) for *S.granarius* and *S.oryzae*, respectively (Howe, 1965). Moisture contents rose to optimal levels towards the end of autumn (advent of cold wet season) but by then the temperature was decreasing to subthreshold levels. On the other hand,

moisture in the successful (Figure 3.3b-d for *S.oryzae* and 3.3d for *S.granarius*) colonies never had any depressive effect on productivity for it remained high (Figure 3.3b-d) throughout the duration of the experiment. A possible explanation for this is given below.

High food to insect ratio may retard population growth as contact between the sexes is minimal (McLagan and Dunn, 1935). The optimal ratio, i.e. quantity of grain/number of insects, is about 20 grains/insect (Evans, 1977) but in this experiment these had been set considerably higher (Section 3.2.2). Once colonisation had been initiated, the moisture content remained high possibly as a result of the respiratory processes of large numbers of insects which liberated metabolic water into the habitat. The humidity resulting from such metabolic water would exert a moderating effect against very hot conditions in the habitat resulting from the combined effect of the heat due to respiratory activities and the very high air temperatures recorded in summer. The retention of metabolic heat would help to maintain more favourable intra-habitat temperatures against environmental subthreshold temperatures in winter (Coombs and Woodroffe, 1963). These fluctuated as those of the surrounding environment in the less vigorous experimental cultures.

The carrying capacity in the high insect densities was reached during the 16th - 20th weeks by which time the food/insect ratio had fallen to about 3.6 grains per insect. The result was that conditions became intensively crowded in the habitats. The population estimates between weeks 12 and 20 indicated that the immature stages outnumbered adult beetles about 2:1. This is based on the number of adults found present at demolition as compared with the progeny harvested from the medium after the adults had been removed. After that time only insignificant numbers of new adults were added to the colonies. With crowding as intense as that observed here infertility in eggs has been shown to increase as excessive contacts prevent copulation and eggs are strewn indiscriminately with some falling in the interstices where they cannot develop (McLagan and Dunn, 1935 and Richards, 1947). Mortality of the immature stages also increases due to accidental injury by adults as they probe every grain for food and for the purpose of oviposition. The larvae may also eliminate each other if there happens to be more than one larva present in each grain at any one time. The end result is an inhibition of further population growth.

The activities of the weevils had resulted in the conversion of wheat into husks, frass (mostly faecal pellets), fragments of endosperm and dead weevils. Eventually the whole population crashed to extinction after the wheat had been reduced to mouldy chunks of solidified "flour". In the unsuccessful colonies, on the other hand, over 60% of the food substrate remained unutilized when most of the insect populations had died out, probably as a result of very high summer temperatures. A few individual beetles were harvested alive in these unsuccessful colonies in January 1979 but only dead weevils were salvaged from the cultures at the end of the experiment in February, 1979.

The total productivity per colony for the successful densities reached average levels of 8,200 adults after 64 weeks. This compares with 80,000 adult *S.granarius*/6 kg of wheat (= 8,000 beetles/600 g wheat) after 2½ years realised by Coombs and Woodroffe (1963).

The results discussed above appear to indicate that, whereas a single pair of weevils could initiate a population at 25°C + 70% R.H. (Surtees, 1964) small weevil densities could not establish a population in nature, under the South Australian weather, at least. Therefore assumption (a), regarding the ability of *Sitophilus* spp to initiate colonies wherever undamaged grain accumulations exist is invalid, except with modifications. It required a minimum density of 30 pairs/ 600 g wheat (*S.oryzae*) and about twice that number for *S.granarius* for colonisation processes to proceed effectively under the conditions of this investigation. In reduced grain bulks (100 g) (Section 2.4) small weevil densities could initiate populations probably because the reduced sizes of the grain bulks permitted frequent amounts of contact between the beetles.

Emigration:

The results shown in Figure 3.3a-d indicates a clear positive correlation between density and emigration. It appears there is a threshold population density below which little or no emigration occurs. Such a threshold was about 800 beetles per colony of *S.granarius* and 500 adults for *S.oryzae*. Once that take off stage had been reached emigration continued except during the cold months when the rates were greatly reduced. When the food supply was nearing complete exhaustion the numbers emigrating exceeded those remaining in the habitats except in the colonies of *S.granarius* (Figure 3.3d). It appears therefore that *S.oryzae* possesses a stronger propensity to emigrate in response to density and other physical conditions in the habitat than *S.granarius*. The intermediate densities of the latter together with the lowest densities of both species (Figure 3.3a-c) in which population growth had been less vigorous no significant amount of emigration occurred.

Figure 3.3a-d failed to show the effects of temperature on the observed emigration patterns. Results of the 2-weekly emigrant recoveries have consequently been presented separately in Figure 3.4 together with the maximum intra-habitat temperatures. It is obvious that until the critical insect density had been reached temperature had

Figure 3.3: Adult population curves showing the proportions of non-emigrants (N-E) and emigrants (E) for *S.granarius* (top) and *S.oryzae* (bottom) together with percent moisture contents of the grain.

Initial densities at onset of experiments:

3.3a - 15♂ + 15♀ beetles/600 g wheat
3.3b - 30♂ + 30♀ " " "
3.3c - 60♂ + 60♀ " " "
3.3d -120♂ +120♀ " " "

●——● (N-E) Number of beetles recovered at demolition time

o-----o (E) Cumulative number of beetles that had emigrated before demolition.

Fig. 3.3a

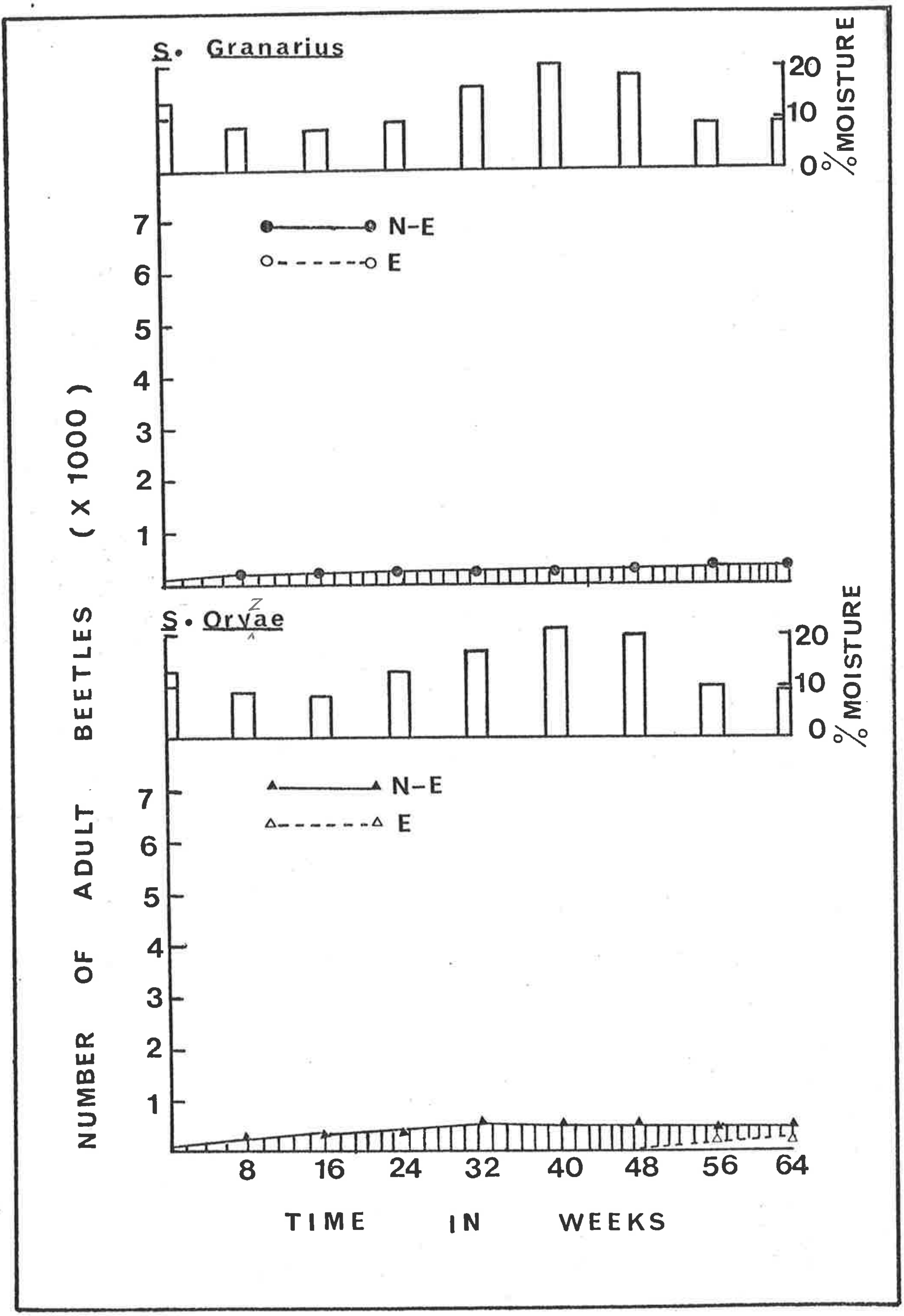

S. Granarius
% MOISTURE
0
10
20
N-E
E
NUMBER OF ADULT BEETLES (X 1000)
1
2
3
4
5
6
7
S. Oryzae
% MOISTURE
0
10
20
N-E
E
1
2
3
4
5
6
7
8
16
24
32
40
48
56
64
TIME IN WEEKS

Fig. 3.3b

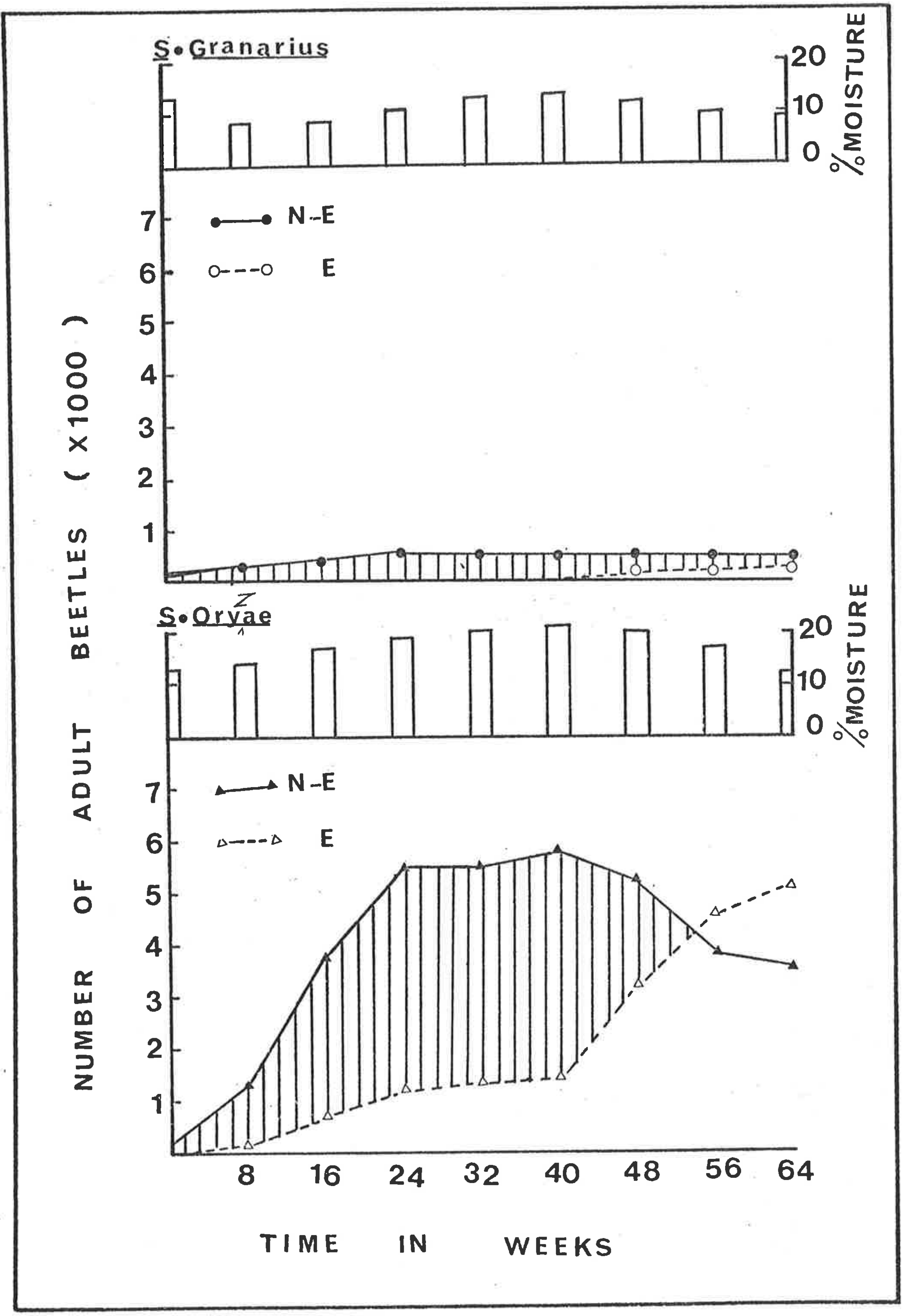
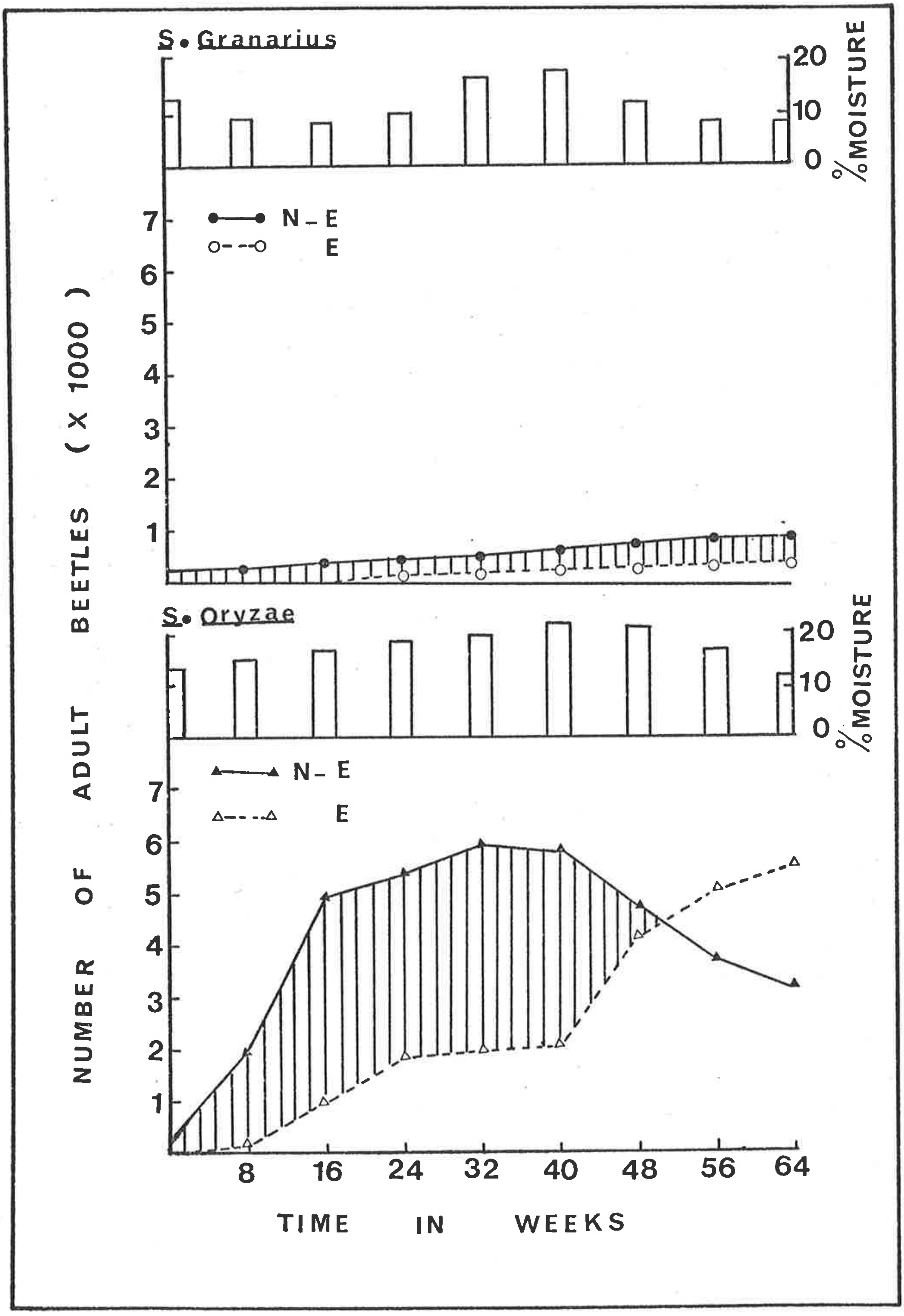

S. Granarius
20
10
0
% MOISTURE
7
6
5
4
3
2
1
N-E
E
NUMBER OF ADULT BEETLES (X1000)
S. Oryzae
20
10
0
% MOISTURE
7
6
5
4
3
2
1
N-E
E
8
16
24
32
40
48
56
64
TIME IN WEEKS

Fig. 3.3c



S. Granarius
20
10
0
% MOISTURE
N - E
E
7
6
5
4
3
2
1
NUMBER OF ADULT BEETLES (X 1000)
S. Oryzae
20
10
0
% MOISTURE
N - E
E
7
6
5
4
3
2
1
8
16
24
32
40
48
56
64
TIME IN WEEKS

Fig. 3.3d

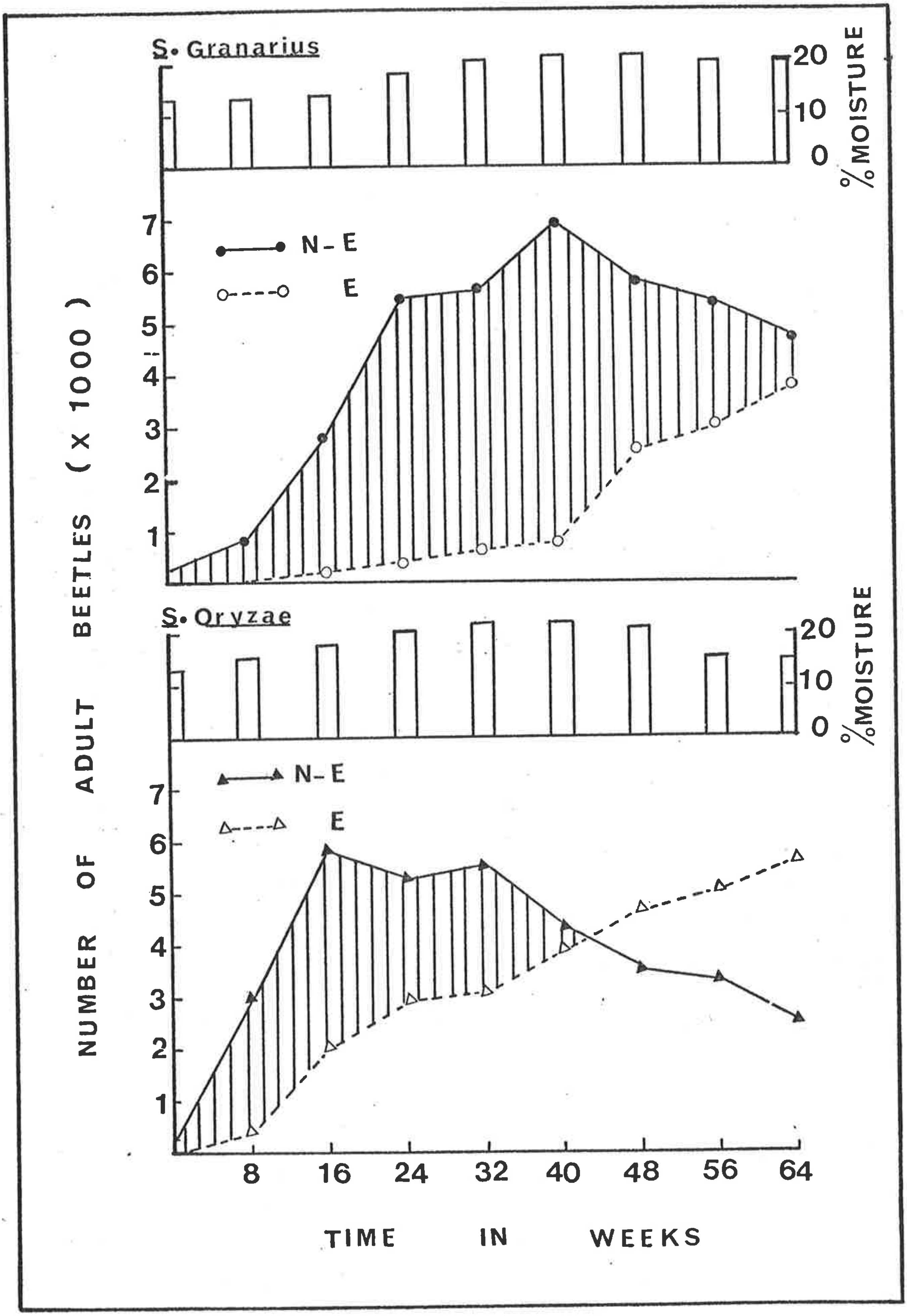
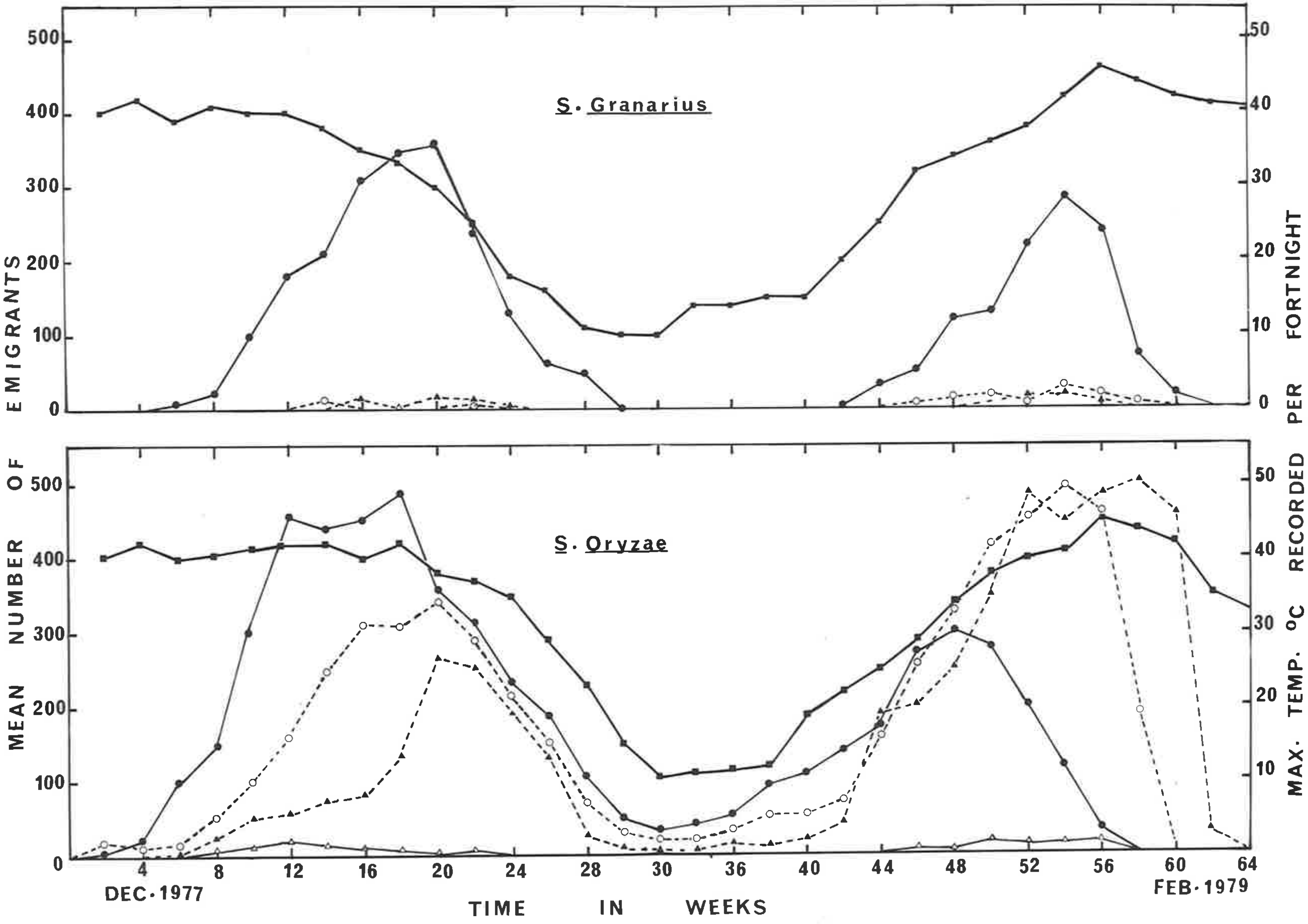

S. Granarius
20
10
0
% MOISTURE
7
6
5
4
3
2
1
N - E
E
NUMBER OF ADULT BEETLES (X 1000)
S. Oryzae
20
10
0
% MOISTURE
7
6
5
4
3
2
1
N - E
E
8
16
24
32
40
48
56
64
TIME IN WEEKS

Figure 3.4: The effect of temperature on the emigration behaviour of *Sitophilus* spp in natural habitats.

Temperature	■—■
120♂ +120♀ in 600g Wheat	●—●
60♂ + 60♀ "	○- - - - - -○
30♂ + 30♀ "	▲- - - - - -▲
15♂ + 15♀ "	△—△


S. Granarius
S. Oryzae
MEAN NUMBER OF EMIGRANTS
MAX. TEMP. °C RECORDED PER FORTNIGHT
0
100
200
300
400
500
0
10
20
30
40
50
4
8
12
16
20
24
28
30
36
40
44
48
52
56
60
64
DEC·1977
FEB·1979
TIME IN WEEKS

little effect on emigration. A clearer relationship was apparent during winter (28th - 42nd) when a significant fall in temperature was followed by a great reduction in the emigration activities notwithstanding the observed high population densities and therefore high intensities of crowding. From then on an increase in temperature with the approach of summer resulted in an increase in emigration until the population crashed to extinction when the grains had been converted to foul chunks of solidified "flour" and frass.

The data on emigrant recoveries for the first eight weeks showed that the proportion of males emigrating was greater than that of the females. However recoveries beyond the 8th week showed no significant differences in the migratory behaviour of the two sexes. Similar findings have been reported by Browning (1947) and Surtees (1964). While investigating population establishment and dispersive behaviour of grain weevils at 25°C and 70% R.H. Surtees (1964) also reported that there were behaviouristic differences between mated and unmated young beetles. By dissecting and examining the contents of the female's spermatheca for the presence or absence of spermotozoa and the maturation status of eggs in the ovarioles and ovaries and the male's vas deferens and vesicula seminalis for the presence of maturation status of spermatozoa he was able to demonstrate that virgin males and females were more dispersive than mated individuals of either sex. His results further revealed that the number of mated females migrating to the top of the grain bulks was comparatively smaller than that of the corresponding category among the males. He attributed this to the fact that mated females spend most of their time below the surface searching for oviposition sites while the upward migration of virgin beetles enhances the chances of meeting between the individual members of the opposite sex. However, this behavioural difference was also short lived for virgin and mated adults behaved alike after five weeks. Rather dissimilar results were reported by Ziegler (1976) among adult flour beetles, *Tribolium* spp, where males were less migratory than females except among very old cohorts. The findings of Surtees and Ziegler accord in one important respect, i.e. young flour and grain beetles are more migratory than older beetles of both genera.

The results on growth and emigration patterns of *Sitophilus* appear to have demonstrated that a colony of either species comprises two classes of beetles, i.e. one group of adult beetles which will emigrate in response to density and temperature and another group which will always remain in the habitats in spite of the deteriorating conditions inside those habitats (Figure 3.3a-d). The population estimates at final demolition showed (see points for week 64 in Figure 3.3a-d) that about 99.8, 71, 68 and 58% of *S.granarius* had not emigrated. The corresponding figures for *S.oryzae* were 74,48,38 and 32%. However, the situation in these continuous cultures was hard to analyse because generations overlapped and many different things were happening simultaneously inside the habitats.

An important conclusion derived from studies in this subsection is that emigration appears to increase temporal stability of the total population in the habitat. For, if that was not the case, 600 g wheat could not be expected to support high population densities for as long as 64 weeks, if their rates of increase (quoted above) were achieved in this experiment.

3.3 Further studies on migratory behaviour

3.3.1 Introduction

Kennedy (1961) has defined migration in terms of enhanced locomotory behaviour which results in persistent, straightened-out movement. Such movements do not have to be in any specific direction as first viewed by Williams (1958). Dingle (1972) reviewed the literature on migration and expressed the opinion that Kennedy (1961); Southwood (1962) and Johnson (1969) had developed an essentially integrated view of the subject although each has emphasized a different aspect. In Kennedy's view for movement to be migratory the insect's movement should not be arrested by any stimulus (e.g. food, mating, oviposition sites, shelter, etc).

The results discussed above (Subsection 3.2) showed that a colony of either species of *Sitophilus* consisted of two discrete classes, namely migrants and non-migrants. However the design of that experiment was such that the observed migratory movements could not be clearly categorised as migration according to the above definition. The beetles could have reached the collection chamber as a result of random movements (or by accidentally falling off the edge of the habitat). If that was actually the case such emigrants could have ultimately found themselves back in their old habitats save for the "Fluon" which barred their re-entry. The object of the observations described here was, therefore, another test to try and verify whether or not a colony of *Sitophilus* comprised migrants, non-migrants or both.

3.3.2 Materials and Methods

A concentric circular arena (Plate 3.22), 1 m diameter was constructed from plywood and its perimeter provided with a fence (5 cm high) coated with "Fluon". The rough side of plywood was painted white to allow easy viewing of beetles under red light.

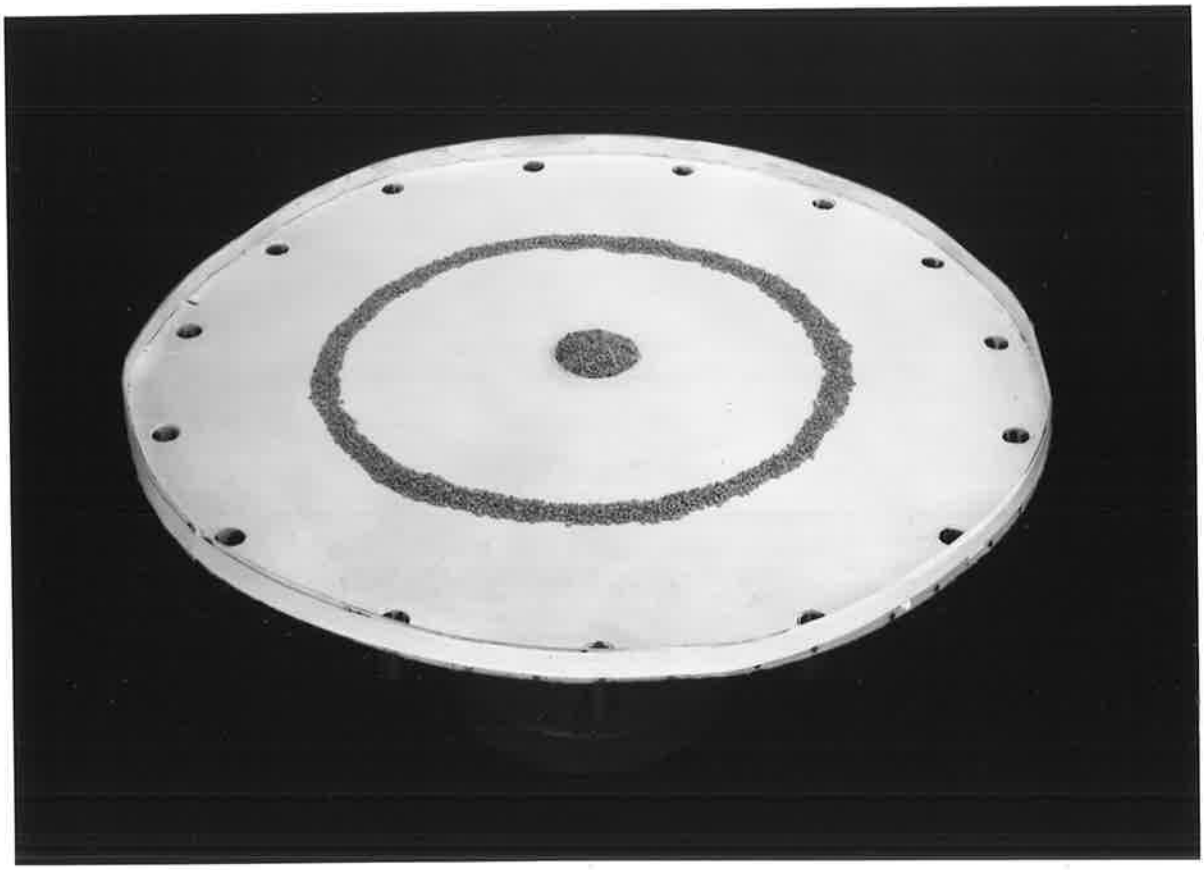
Plate 3.22: Arena used to study migratory behaviour of grain weevils.

<u>Experimental habitat</u> (centre of arena)

Ring of fresh grain (between edge of arena and habitat).

Pitfall traps near the edge of arena (not used in this observation).

Fence with a band of "Fluon" at edge of arena.



At the centre of the arena was a hole in which a 200 g polystyrene jar containing experimental cultures could be securely fitted in so that its mouth was level with the surface of the arena. This apparatus was held in the 30°C constant temperature room on top of the open side of a dust bin so that individual jars could be inserted and removed with ease. A ring consisting of a thin layer of grain was placed on the arena, half way between the centre and the edge. Beetles moving out in response to density pressure or in search of fresh food or oviposition sites should respond to the fresh grain. If they were true migrants, according to Kennedy's definition, they should walk past the ring.

Experimental cultures were started by inoculating 5 replicates of 150 g of wheat with 150 pairs/culture of either species. These were reared at 30°C and 70% R.H. After 6 weeks of breeding, that is when a new generation of adult beetles was being added to the colonies (thereby increasing the intensity of crowding) the observations commenced. Each jar containing test beetles was inserted into the hole and kept covered for 24 hours to allow the beetles to recover from the disturbance after which the cover was cautiously removed and the movement of beetles studied under red light which had proved to have no effect on their dispersal behaviour, a finding originally reported by Surtees (1963a).

3.3.3 Results and Discussion

Many beetles moved out of the grain of their own accord either continued moving outwards in all directions or wandered about their immediate surroundings and then returned into their old habitats.

Footnote: Attempts to study migratory behaviour with a Time-lapse camera fitted with a flash light were unsuccessful.

For convenience I have elected to use the following terms to describe different behavioural patterns:

1). <u>True migrants (TM)</u> - those individual beetles which exhibited persistent, straightened out movements.
2). <u>Potential migrants (PM)</u> - those individuals which moved out but whose movements were arrested by the ring of fresh grain.
3). <u>Non-migrants (Non-M)</u> - those beetles which moved out, wandered about and returned to the old habitats. This category includes those beetles which never left the habitat.

The results of the studies on migration behaviour are summarized in Table 3.6. These have been presented as total numbers observed in each category together with (in brackets) the mean and standard error (S.E.) for the 5 replicates of either species and the relative frequencies (RF, that is, relative to the total). The results have been subjected to a X^2 test to verify the apparent differences in migratory behaviour between the two species.

Table 3.6: Total number of beetles per category, the mean ± S.E., relative frequencies and the value of X^2 test for comparison of migratory behaviour of *S.granarius* and *S.oryzae*. n = 5.

	Behaviour Categories			
Species	TM(True Migrants)	PM(Potential Migrants)	Non-M (Non-Migrants)	Total
S.granarius	839 (104.9 ± 4.5)	28 (3.5 ± 0.8)	701 (87.6 ± 3.6)	1568
RF	0.535	0.018	0.447	
S.oryzae	891 (111.4 ± 3.8)	606 (75.8 ± 3.4)	313 (39.1 ± 5.2)	1810
RF	0.492	0.335	0.173	

Test Chi– Square = 660 ~~66.0409~~ with 2 d.f.

The difference is highly significant at P = 0.010, thus indicating that the two species differ signficantly with respect to their migratory behaviour. It has already been demonstrated (Section 3.2) that *S.oryzae* exhibits a stronger propensity to emigrate in response to density and diminishing food resources than *S.granarius*. It has also been shown in this section that the proportion of non-migrants was only 0.173 for *S.oryzae* compared with 0.447 for *S.granarius*. However, of the proportions that had taken off there were more true migrants (96.8%) for the latter species compared with (59.5%) for the former.

Since potential migrants cannot be classified as migrants according to the definition of Kennedy the proportions of true migrants among the observed emigrants (Figure 3.3d) may now be corrected using the percentages shown above. Thus the proportions of true migrants among the emigrants in Figure 3.3d would have been 57% and 40% for *S.granarius* and *S.oryzae*, respectively. The implication of the foregoing would be that in the absence of density pressures or other ecological stimuli which may force the emigration of large numbers of beetles (true and potential migrants alike) a colony of *S.granarius* would produce more migrants than that of *S.oryzae* under identical conditions.

3.4 Food searching Behaviour

3.4.1 Introduction

Section I made reference to Levinson and Levinson (1979) report to the effect that food may be used as an attractant to lure stored grain pests into aggregations where chemicals can then be profitably applied to control them. This would appear to imply that these species must be able to respond to the food stimuli in the vicinity of their habitats. However a search through the voluminous literature on the dynamics of *Sitophilus* spp has not revealed information about the reaction of either species to food odours in their environment.

An investigation ought to begin with an attempt to demonstrate that olfactory senses play an important role in enabling *Sitophilus* species locate their food sources in nature. The objective of this study was therefore to investigate the response of adult beetles of either species to a source of odour, namely a food substrate (wheat).

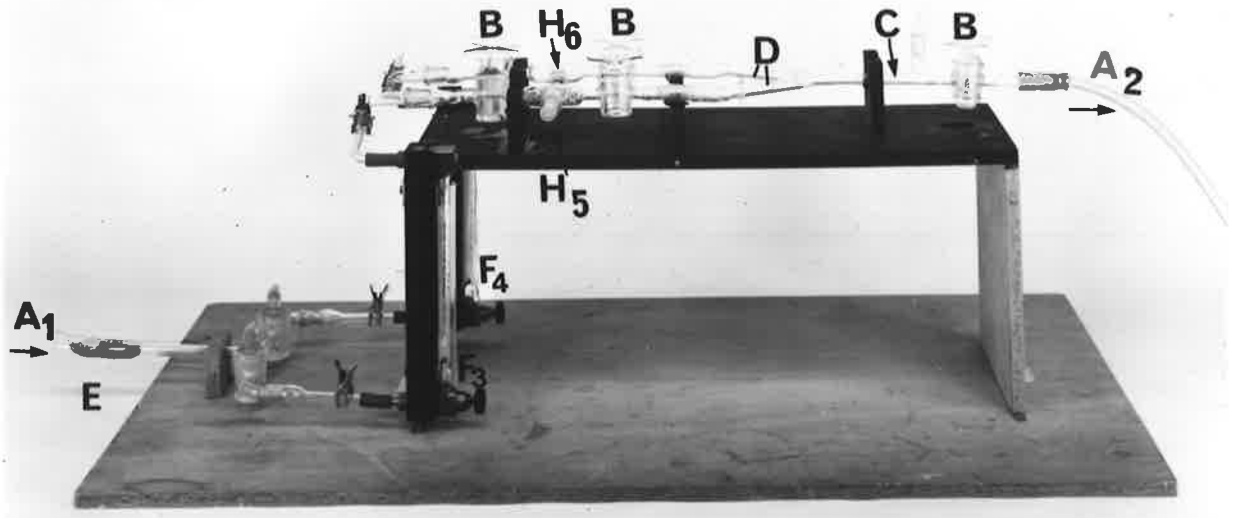
3.4.2 Materials and Methods

A binary - choice olfactometer (Plate 3.23) was constructed so that an air-current could be drawn through a filter (activated charcoal) to remove impurities. The air current could then be divided into two equal streams regulated by means of adjustable flow-meters and drawn across the two arms of the Y-tube then out through the suction tube. The importance of an air stream in enabling crawling Coleoptera to exhibit directed response to attractive materials has been stressed by Jantz and Rudinsky (1965). The two arms of the Y-tube house two chambers, one of which could contain the food substrate while the other remained empty as control. The joined part of the Y-tube houses a third chamber in which the test insects could be introduced.

Test beetles, reared by the technique described in Section 3.2, were studied at 30°C and various R.H. under red light. In every experiment 25 test beetles were used per cohort and these were replicated 5 times.

Plate 3.23: A binary - choice oflactometer.

A_1 = Air intake
A_2 = Air outlet (tube connected to suction pump)
B = Regulatory stopcocks
C = Chamber for test insects
D = Y-tube
E = Activated charcoal
F_3 and F_4 = Airflow meters
H_5 and H_6 = Chambers for bioassay materials.


B
H6
B
D
C
B
A2
H5
F4
A1
F3
E

3.4.3 Results and Discussions

The experiments were started with dry wheat of 9.5, 10.5, 11.0, 12.0% moisture contents (m.c.) (simulating grain spillages in warehouses) as the food substrate and then continued with conditioned wheat (conditioning method as in Section 2.3.1).

As shown in Table 3.7 beetles of both species were unable to discriminate between scented and unscented air-streams when dry wheat was used as the substrate. The proportions of beetles responding to either scented or unscented air-streams were about the same. However that behaviour was altered substantially when conditioned wheat (m.c. 13.5, 14.2, 15.8%) was used as the stimulus. There were no significant differences in the observed responses at 13.5-15.8% moisture levels. Consequently responses observed at 14.2% m.c. have been taken to represent the reactions of beetles to conditioned wheat substrate. The values of the standard error indicated that there was variation between the replicates of either species; the degree of variability being wider among those replicates of *S.oryzae* than among those of *S.granarius*. The latter species appeared to exhibit a very strong positive response to conditioned wheat odours compared with a rather moderate positive response exhibited by *S.oryzae*. The number of negative responses slightly increased with the age of the beetles in *S.oryzae* ($X^2_{\cancel{6}\,3}$ = 16.531, significant at P = 0.05).

This investigation has indicated that most adult grain and rice weevils can respond to wheat odours by walking towards the wheat accumulations. The relative humidity of the air blowing over the grain appears to have a critical role in determining whether or not the weevil's olfactory senses will identify the

Table 3.7 Summary of responses of adult *S.granarius* and *S.oryzae* to scented (Stimulus) and unscented air-streams (Control) at 30^{o}C & 11% m.c. and 30^{o}C and 14.2% m.c. (n = 5)

Dry wheat of 11% m.c.		Number and type of response (mean ± SE)		
Species	Age in days	+(towards stimulus)	-(towards control)	Total
S.granarius	7	67 (13.4 ± 1.4)	58 (11.6 ± 1.4)	125
	14	61 (12.2 ± 2.0)	64 (12.8 ± 2.0)	125
	28	63 (12.6 ± 1.6)	62 (12.4 ± 1.6)	125
	42	not tested	not tested	-
S.oryzae	7	62 (12.4 ± 1.2)	63 (12.6 ± 1.2)	125
	14	53 (10.6 ± 2.1)	72 (14.4 ± 2.1)	125
	28	64 (12.8 ± 2.5)	61 (12.2 ± 2.5)	125
	42	not tested	not tested	-

Wheat of 14.2% m.c.

S.granarius	7	95 (19.0 ± 0.7)	30 (6.0 ± 0.7)	125
	14	95 (19.0 ± 0.6)	30 (6.0 ± 0.6)	125
	28	91 (18.2 ± 1.1)	34 (6.8 ± 0.4)	125
	42	92 (18.6 ± 1.1)	32 (6.2 ± 1.1)	125
S.oryzae	7	90 (18.0 ± 0.0)	35 (7.0 ± 1.0)	125
	14	83 (16.6 ± 1.3)	42 (8.4 ± 1.3)	125
	28	78 (15.6 ± 1.2)	47 (9.4 ± 1.2)	125
	42	62 (12.4 ± 0.9)	63 (13.2 ± 1.3)	125

substrate odours. They appear to be unable to smell grain drier than 12.0% m.c. Grain is normally harvested when the moisture content is between 13 and 14% and this level further declines to about 11% while in storage or even lower as in spillages during the dry season. Ecologically, the problem is to explain how the beetles find grains that are drier than 12%m.c., especially in hot dry weather. A possible explanation may be found in their dispersal behaviour which appears to be random (Section 3.3) in dark warehouses. The wandering pattern of their movements in darkness may lead individual weevils to the sources of grain spillage.

3.5 Summary

In small bulks of dry grain success in initiating an infestation depends on the density of beetles present to create buffer conditions against adverse weather conditions of the environment. 600 g wheat may support a population size of about 8,000 beetles providing emigration occurs.

A colony of either species comprises emigrants and non-emigrants. Emigration is density- and temperature-dependent. But in cold weather emigration is minimal notwithstanding high weevil densities present in the habitats. A colony of *S.granarius* would be expected to produce more true migrants than that of *S.oryzae* under identical optimal conditions.

Adult *Sitophilus* find food for themselves and their progeny by means of olfactory senses. However the moisture content of the food substrate is critical. They do not appear to have the capacity to locate food drier than 12% moisture.

4. DYNAMICS OF AN ENDEMIC WAREHOUSE POPULATION OF *S.ORYZAE* BREEDING IN UNDISTURBED GRAIN BULKS

4.1 Introduction

It is widely believed that pockets of grain which are left lying undisturbed in corners, cracks, crevices and in harvesting machinery for long periods of time will provide, if weevils find their way and start to breed in them, sources of infestation for new-crop grain (Coombs, 1956; Munro, 1966; McFarlane, 1968).

While carrying out a survey (Section 1) to determine the incidence of occurrence of *Sitophilus* spp in the State I found that a warehouse situated near Moorook harboured an endemic population of *S.oryzae*. This resident population had been breeding in chemically treated barley and wheat contained in six bags which had been stacked on the unsealed ground floor of a shed and left undisturbed for several years. With the passage of time the insecticide compound had lost its efficacy probably due to degradation thus leaving the grain vulnerable to attack by *S.oryzae* and other primary pests of stored grain. This resident infestation offered an ideal opportunity to make observations on the species population dynamics with particular emphasis on the interactions between the widely fluctuating environmental factors, change in the quality of food with time, dispersal and effects of the presence of other insect pests living on the same medium. Such information would constitute an essential basis for the understanding of the species dispersal behaviour in a field study to be reported in Section 5.

The experiments of Coombs and Woodroffe (1963a, 1968 and 1973) on ecological succession among stored grain pests were carried out in confinement and hence it was possible to take samples periodically in order to estimate the numbers of each species present in the experimental habitats and to determine the degree of disintegration of the wheat medium. Such samples could then be reconstituted and returned to their respective places in the habitats. In the work reported here the infestation was not in confinement and therefore emigration and immigration of this species or other species were possible. No attempt was made to obtain direct information on the absolute numbers of immature and adult beetles present in the grain at any specific time since any sampling technique that disturbs both insects and medium triggers mass emigration (Barnes and Grove, 1916) and tends to make subsequent results unreliable (Surtees, 1963a).

4.2 Materials and Methods

By using window and pitfall trapping an estimate of seasonal fluctuations in numbers and the modes of dispersal of *S.oryzae* in its natural environment could be obtained. Chapman and Kinghorn (1955) and Southwood (1966) have shown that flying Coleoptera and other insects that fall on hitting an obstacle during flight could be sampled with a window trap. They also suggested substituting a rigid transparent plastic for glass so that the wooden frame could be eliminated resulting in an unbreakable trap which could be used under field conditions for any season. The harsh environmental conditions (including wind storms) coupled with the likelihood of accidents by wandering domestic animals and children justified the substitution of clear perspex for glass.

The modified trap consisted of a perspex sheet (45 cm x 30 cm) suspended by a rope which connected it to a plastic trough containing alcohol + glycerol as the collecting fluid. Above the perspex was a black polypropylene cone (50 cm diameter) whose function was to prevent beetles reaching the trough by walking along the crossbars of the shed and then down along the rope. A dozen traps were then hung at different heights (0.5 - 2.5 m) above and surrounding the infestation.

Fifty pitfall traps (polystyrene tubes 7.5 cm deep x 2.5 cm mouth diameter) were sunk into the ground at a radius of 2.0 m from the infested grain. The aim of this was to monitor the species migratory activities and relate such movements to the components of the environment. A mixture of glycerol and alcohol was added to the traps to preserve the catch. A Honeywell thermocouple was used to record changes in the temperature of the grain. A thermoghgrograph recorded ambient temperature and relative humidity. The catch was emptied and recorded at fortnightly intervals.

4.3 Results and Discussions

It was not known when the infestation commenced but examination of a sample of grain taken in March 1977 indicated that weevils had been breeding there for several months. The experiment did not begin until September 1977 when beetles started reappearing after the cold winter weather which appears to restrict reproductive and emigratory activities (Sections 2 and 3) and makes adult beetles move to the lower and perhaps warmer depths of the grain accumulation.

The window traps were designed to provide evidence of the species capacity to disperse by flight. However no weevils were caught during the 21 months observations, except for three, caught in two traps, in the period 5 - 19 November, 14 months after the observations began. A wide variety of other flying arthropods were always recovered in the window traps throughout the experimental period. The recovery of three rice weevils coincided with a wind storm experienced on November 11. The storm blew a lot of litter into the traps. It is therefore difficult to conclude that the three rice weevils constituted evidence of flight by *S.oryzae* for it is most probable that they were simply blown off the surface of the bags or floor into those two traps. If these beetles were able to disperse by flight the probably of that occurring was greatest during the months of December and January when massive numbers of weevils were sighted.

Using a similar technique Giles (1969) was able to recover many adult *Sitophilus zeamais* but no *S.oryzae*, notwithstanding evidence of its presence in grain stored in that warehouse. Taylor (1970) used a suction trap and recovered large catches of *S.zeamais* and a few *S.oryzae* beetles (1% of the total recovery).

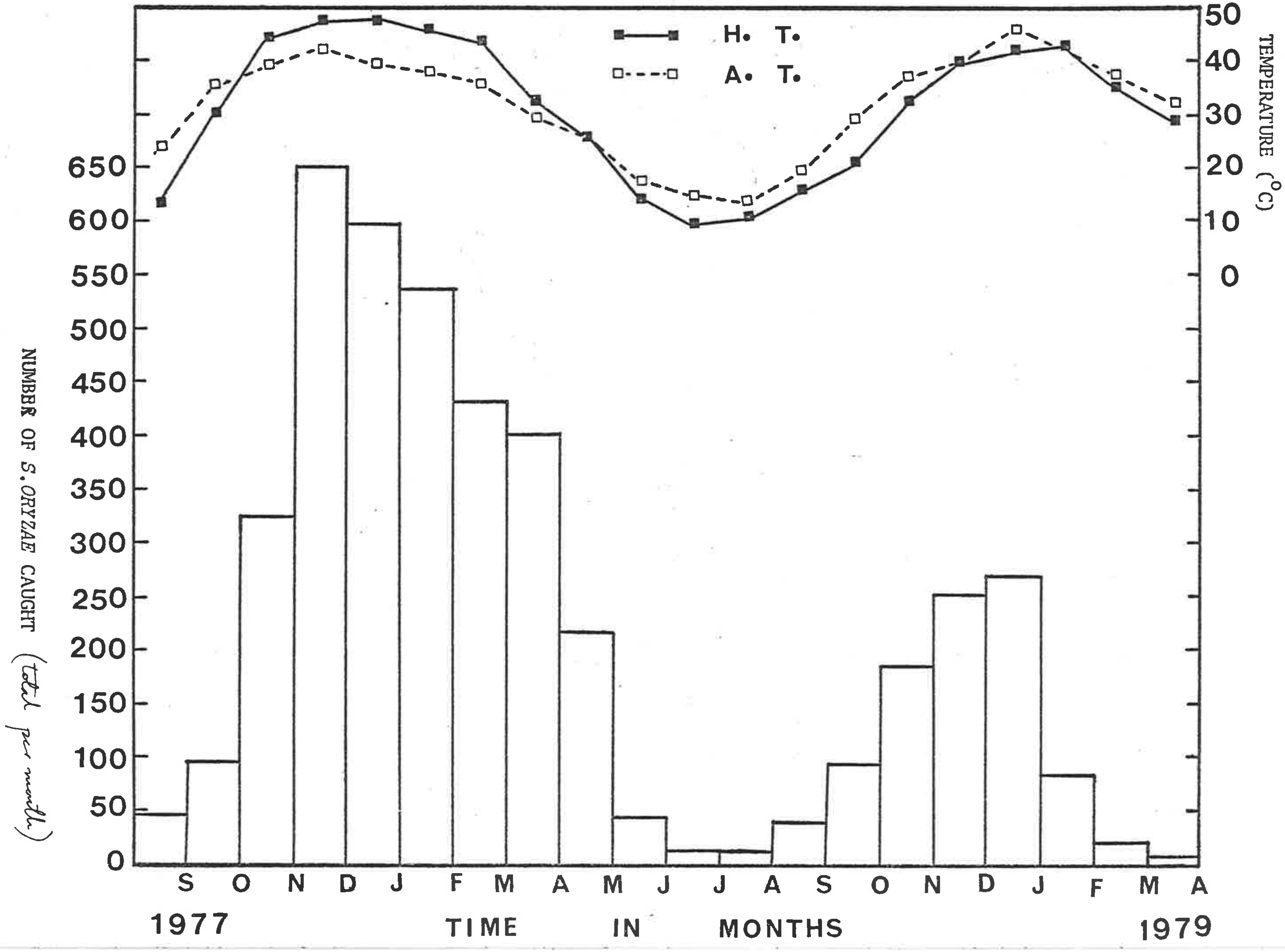
The monthly total number of weevils recovered from the fifty pitfall traps are shown in the histogram (Figure 4.1). As predicted there was a correlation between temperature and migration. As temperature increased to optimal and above optimal levels in spring and summer, respectively, there was an upward migration of beetles to the surface of the grain. Very large numbers of weevils could be seen crawling on the surface of the bags and on the corrugated asbestos sheets which formed a wind-break on the eastern wall. The number of beetles recovered from the pitfall traps increased to reach a peak of about 650 beetles per month in the summer of 1977-78, and another, though comparatively smaller, peak during the corresponding period in 1978-79. During the cold winter months migratory activities were at their lowest level, and during that time few or no weevils could be seen on the surface of the grain. The smaller peak of about 250 observed in the summer of 1978-79 was followed by a rapid decline in numbers of adult *S.oryzae*. It was not possible to see what effect the temperature of 46°C recorded in January 1979 had on the observed sharp population decline. Although the observations continued until December 1979 no rice weevils were caught after April 1979.

Relationship between temperature
+ migration activities

Figure 4.1 ~~— Total number of adult *S.oryzae* caught per month and the corresponding maximum 2-hourly ambient and grain temperatures recorded during that month.~~

■—■ H.T. - habitat temperature

□---□ A.T. - ambient temperature


H. T.
A. T.
50
40
30
20
10
0
TEMPERATURE (°C)
650
600
550
500
450
400
350
300
250
200
150
100
50
0
NUMBER OF S. ORYZAE CAUGHT (total per month)
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
1977
TIME IN MONTHS
1979

Death of a colony of *Sitophilus* may be explained by the species habits. Weevils lay their eggs which complete development (egg - adult) inside the grains and reproduction ceases when no whole grains remain. That the *Sitophilus* populations in the previous chapter (Section 3.4) and in this section should stop increasing after periods of intensive breeding and then die out was, therefore, to be expected. Taken together with the fact that husk and frass are unacceptable as food to *Sitophilus* spp (Coombs and Woodroffe, 1963) it was not surprising that the crash to extinction was rather sudden. What was less clear was the contribution to this rapid decline to extinction made by the invasion of the same food material by the moth *Ephestia cautella* and a group of secondary beetle pests of damaged grain; namely *Cryptolestes* sp, *Tribolium confusum* and *Ptinus tectus*. Andrewartha and Birch (1954), and Varley *et al.* (1973) have indicated that when two or more species compete for the same resource in a culture usually only one survives and the others become extinct. They have also indicated that co-existence is possible in certain species provided that one species does not harm the others. *T.confusum* and *P.tectus* are known to be both predatory and scavenging. *T.confusum* was first sighted in December 1977, and its population had grown to rival that of *S.oryzae* by the end of December 1978. This species has been shown to have a small capacity to emigrate which usually stops when its numbers are low (Ziegler, 1976). Consequently the pitfall traps recovered an insignificant number of this species in spite of the heavy build-up in numbers of adult, larval and pupal stages seen in the grain. The population of the other "camp-followers" of *Sitophilus* and *Ephestia* spp remained too small to cause pest outbreaks. Although *Ephestia* was always present along with *S.oryzae* ~~but~~ its population was not determined.

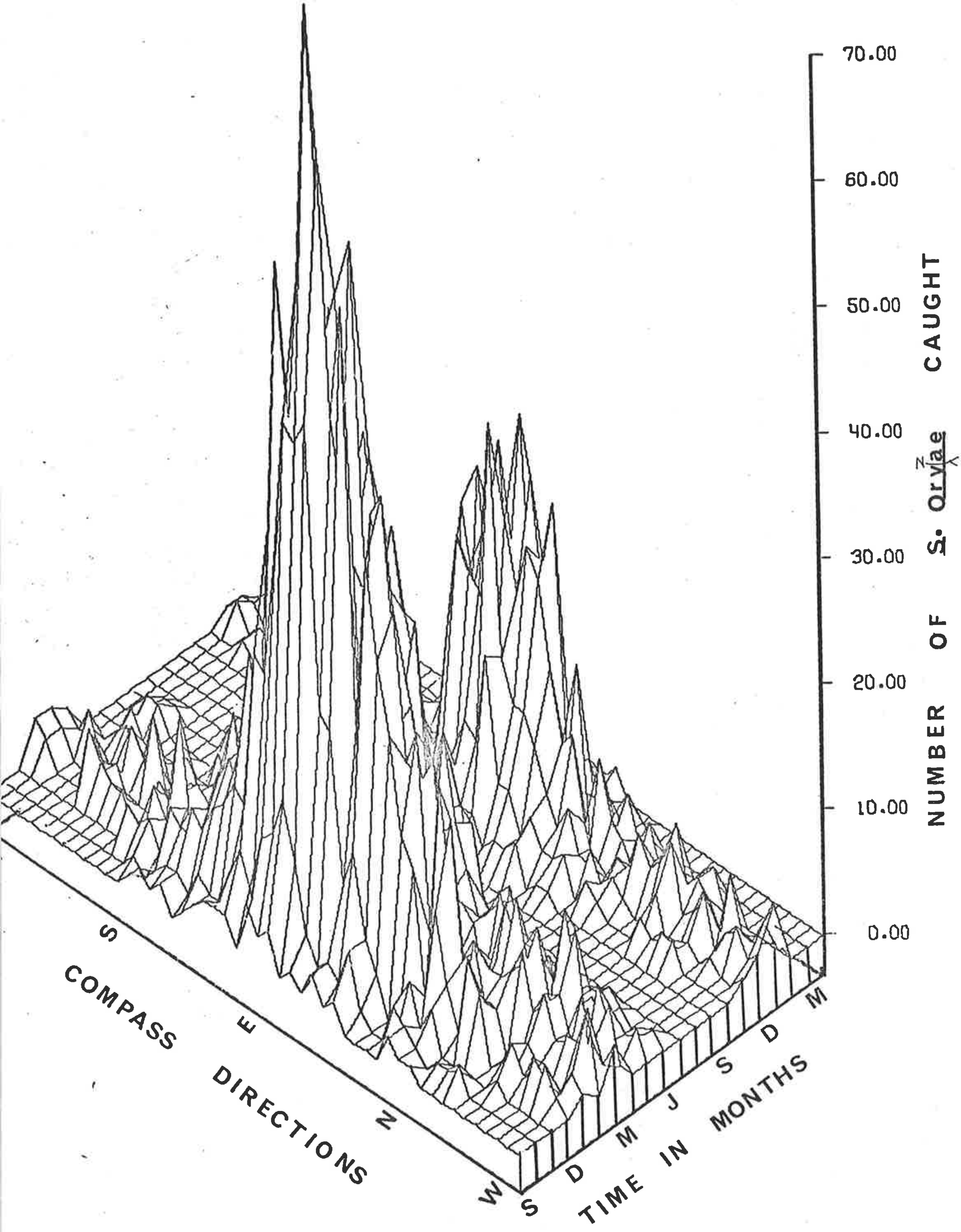
Although this experiment was not designed to study ecological succession, the results show some similarities to those of Coombs and Woodroofe (1963, 1968, 1973). These workers found that altough most of the species were found in grain samples, there was evidence that dominance by certain species was associated with the quality of food. When the grain residues comprised whole grains *Sitophilus granarius* and the moth *Hofmannophila pseudospretella* predominated. If most of the grain was damaged or had been reduced almost to flour *Ptinus tectus* and *Tene*$\overset{rio}{biro}$ *molitor* became the dominant species.

The present observation provided an opportunity to study the distribution patterns of dispersing adult *S.oryzae* in their natural environment. In this context it was of interest to determine whether dispersal of this species was random in directions, and if not, to what extent the shade provided by the only shaded wall (E) might have influenced the observed pattern. As shown in Figure 4.2 the dispersal pattern was not uniform with respect to compass directions. In fact the results appear to have demonstrated that dispersal was significantly directional. The traps located in the NE-SE quarter of the annulus accounted for about 90% of the catch over the entire duration of the experiment while some traps on the western side caught none.

Since the only difference between the compass directions was the presence of a shaded spot in the E it would appear that the observed eastward drift of migrant beetles was in direct response to the darkened spot. Such an inference would tend to accord with the observations of Dendy and Elkington (1920) who reported that *Sitophilus* species shun light and therefore would migrate towards darkness. However, this may be an over-simplification of what was happening to this resident infestation.

The results on migratory behaviour of *Sitophilus* spp described in Section 3.3 above indicated that the movements of these species under dim red light were random. If this is typical behaviour of both laboratory and field populations of *Sitophilus* spp th$\overset{e}{\cancel{a}}$n the observed migratory patterns (Figure 4.2) should not have indicated such a strong directional effect. For in darkness (night time) the apparent response to the shade should have been altered in favour of more random patterns. Further discussions on the effects of light and shade on the dispersal behaviour of *Sitophilus* spp will be found in Section 5.3.3.

Figure 4.2 Three-dimensional representation of monthly catches of *S.oryzae* showing time, directions and dispersal patterns from a resident infestation.


70.00
60.00
50.00
40.00
30.00
20.00
10.00
0.00
NUMBER OF S. Oryzae CAUGHT
S
E
N
W
COMPASS DIRECTIONS
S
D
M
J
S
D
M
TIME IN MONTHS

5 CAPACITY FOR DISPERSAL

5.1 Introduction

Both *Sitophilus granarius* and *S.oryzae* are widely distributed on farm properties throughout the grain belt of the State and control measures based on the use of chemicals are meeting with decreasing success because of increasing resistance of these pests to chemicals (Freeman, 1974; Champ, 1977). It has, therefore, become essential to rely on preventive measures as a more effective technique for combating grain infestations by *Sitophilus*. For this technique to succeed a full understanding of the behaviour, including their capacity for dispersal under field conditions, was essential. Knowledge of the ability of these two species of *Sitophilus* to breed in a standing grain crop prior to harvest, their ability to disperse in the field, and the mechanisms by which they achieve this was lacking.

Dispersal is an important parameter of most animal populations. It may determine the capacity of a population to use scattered food resources, or it may enable a prey species to survive heavy predation (Andrewartha & Birch, 1954; Huffaker, Shea & Herman, 1963). The capacity for dispersal may determine the success of *Sitophilus* in avoiding unfavourable physical changes in their habitats and, indeed, their ability to invade previously uninfested grain crops. It was of interest, therefore, to investigate the extent to which the dispersal behaviour of *S.granarius* and *S.oryzae* can lead to a redistribution of individuals and to determine the mechanisms by which they achieve this, and the rates at which they spread in the field. A further objective of this study was to compare the two species' abilities to colonise standing cereal crops before harvest and to determine the stage of grain maturity (% moisture content) when they were able to do so, for this may very well determine their statuses as field pests and not just pests of stored grain.

Andrewartha and Birch (1954, p.86) have defined dispersal as "movement away from a populated place, resulting in the scattering of at least some of the original population". This definition is essentially the same as that of Southwood (1966, p.256): "The term dispersal covers any movement away from an aggregation or population...". The following definition from Laughlin (1977-78, p.98) has been used in this study: "Dispersal is a term which seeks to describe, quantitatively, the amount of travelling undertaken by members of a species during their lifetime".

In the case of *Sitophilus* spp the immature stages are excluded from active dispersal activities for their whole developmental life is spent in confinement inside the individual grains. These pre-adult stages together with adult beetles, may be transported passively across their ecological barriers as a result of grain trade and other physical means.

Birch (1946); Howe (1951) and Surtees (1963a, 1964a,b and c) investigated the movement or dispersal behaviour of *Sitophilus* inside grain bulks under constant conditions of grain moisture and temperature. The present study was concerned primarily with the type of dispersal which enables the individual weevils to move from one habitat to another, or from one grain storage area to another.

For the purpose of providing the necessary linkages between sub-sections, this section has been arranged as follows:

5.2 Materials and Methods

5.2.0 Can Sitophilus breed in a standing wheat crop?

5.2.1 Laboratory observations to establish the modes and rates of dispersal for each species.

5.2.2 Description of experimental sites.

5.2.3 Trapping and sampling techniques.

5.2.4 Experimental cultures.

5.3 Results and Discussions

5.3.1 Behaviour of weevils after release.

5.3.2 Recovery and ~~M~~mortality.

5.3.3 Spatial distribution and ~~R~~rates of ~~D~~dispersal.

5.3.4 Capacity for colonising grain in the ears.

5.4 Conclusion

5.2 Materials and Methods

5.2.1 Laboratory observations on the modes and rates of dispersal

The two species differ significantly in wing morphology and consequently I had expected different results in their mechanisms and rates of dispersal.

Adult *S.granarius* are large (3-5 mm long) apterous beetles (Cotton, 1950; Munro, 1966) and their method of movement is by walking. *S.oryzae* are comparatively smaller in size (2-3.5 mm long) and possess normal functional wings (Murray and Tieg, 1935; Taylor 1971; Anon. 1978). Evidence of their ability to disperse by flight is lacking and consequently I set out to test the capacity of *S.oryzae* to disperse by flight.

Flight tests were carried out in a flight chamber (Laughlin, 1974) at temperatures ranging from 28-40°C and light intensities of 1.85 and 2.6 lumens/sq. ft. ~~feet~~ (Eel photometer). The insects used in this experiment were the 6th generation of parents originally collected from endemic infestations on farms, and reared on Olympic *8156 soft wheat at 29°C and 70% R.H. Because I had expected flight, if *S.oryzae* was able to fly at all, to occur in those individuals reared under high density or intensity of crowding, I reared my test cohorts at 29°C and 70% R.H. (14% m.c.) using the following densities:

1 pair/40 grains; 2 pairs/40 grains;
4 pairs/40 grains; 8 pairs/40 grains;
16 pairs/40 grains; and 32 pairs/40 grains.

These were replicated 4 times. Ten adult weevils (5♂ + 5♀) from each replicate/density and aged 7, 14 and 28 days were released in the chamber and observed for flight behaviour under different wind conditions to provide different degrees of agitation. My criterion for flight potential was the opening of the elytra and wings.

The results were negative for all densities tested. It is interesting to note that Bishara (1968) reported some flight activity in 4 week-old adult beetles of *S.oryzae* but even then only a strain from Argentina showed this ability at 30-40°C and 1.85 lumens/sq. ft. ~~feet~~. The strains from other countries showed no ability to fly. Bishara's investigation showed that temperature and light intensity are vital factors in the flight behaviour of *S.oryzae* and that of a related species *S.zeamais* Motch. The latter is a well-known flier and common pest of both stored grain and maturing grain in the field (Gurney, 1918; Kiritani, 1959; Giles, 1969; Floyd, 1965 and Taylor, 1971).

The next series of tests were carried out in a 30°C constant temperature room. Under Ultra-violet light 1 in 20 adult (3-5 week old) weevils from the highest density showed some potential for flight. At 30°C and 2.8 lumens/sq. ~~feet~~ ft. these weevils (1 in 20) opened their elytra and hind-wings, departed by making an initial short leap, about 10 cm long and then proceeded only by walking. These observations confirm Kiritani's (1959) conclusion that *S.oryzae* has lost the power to fly, notwithstanding the evidence of presence of normal flight muscles in this species (Murray & Tiegs, 1935; Taylor, 1971). The development of these flight muscles in *S.oryzae* is completed, some time after the emergence of the adult and this delayed completion may account for loss of the ability to fly in some Coleoptera including *S.oryzae (= Calandra oryzae)* (Smith, 1964). The question of whether or not *S.oryzae* flies remains controversial but even if it is able to do so under certain conditions such flights would be a rare occurrence in nature for they have not been observed and verified under normal conditions by Murray & Tieg (1935); Giles (1969) and by me throughout this project. The opening of the elytra and wings observed under strong UV light is a clear demonstration that this species possesses normal functional wings but they are not readily used for normal dispersal purposes. As a consequence of this the study reported in this section involves dispersal by walking for both species.

Figure 5.2.1: Map showing the dimensions of the field of wheat at Mortlock Experiment Station and the compass directions -

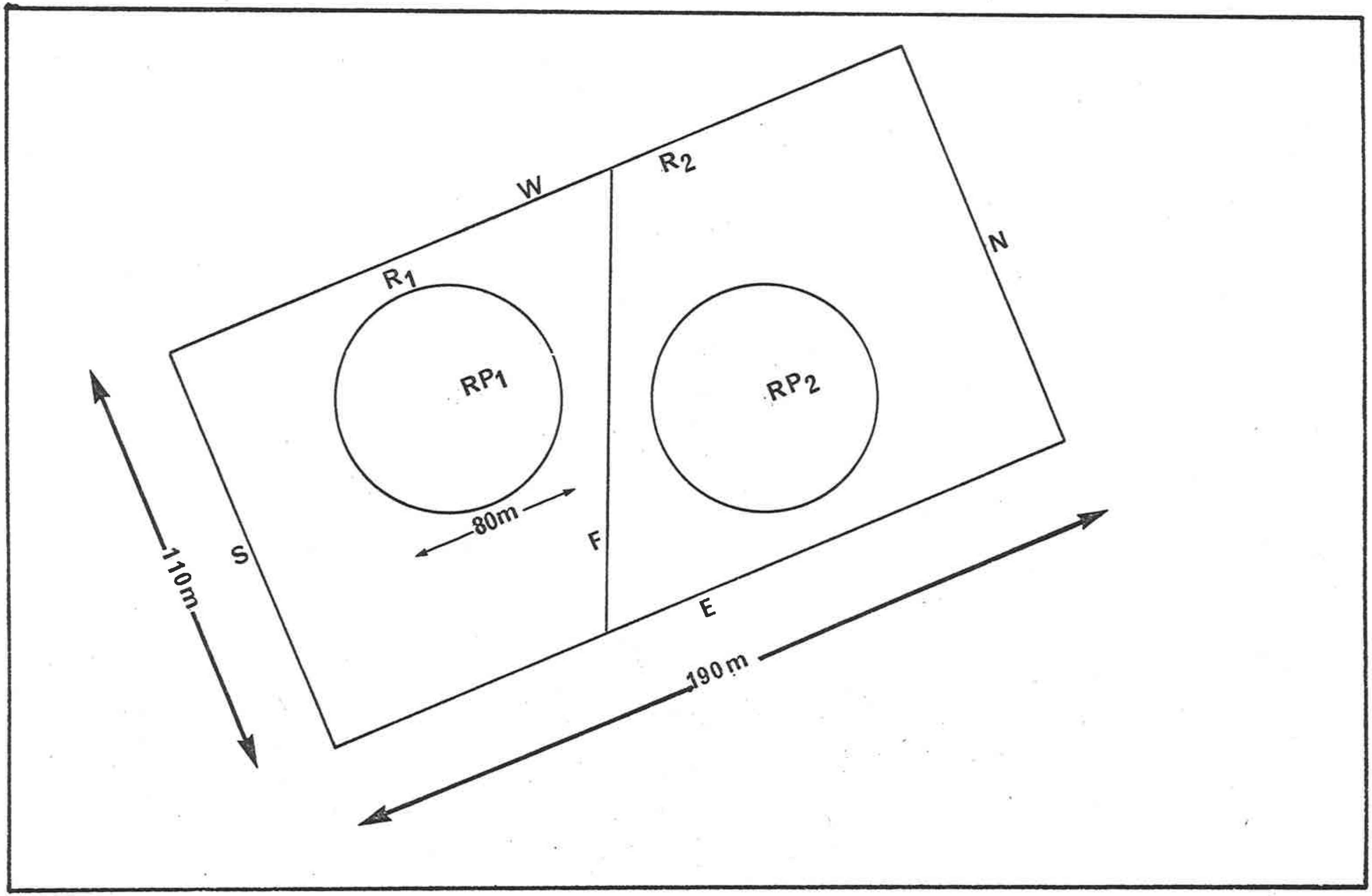
R_1 - Replicate 1

R_2 - Replicate 2

RP_1 - Release point (R_1)

RP_2 - Release point (R_2)

F - Galvanised iron strip fence situated 5 m from either plot.


W
R1
R2
N
RP1
RP2
80m
S
F
110m
E
190m

In the laboratory *S.granarius* walked at an average rate of 25 cm/minute which was equivalent to 360 m/day. *S.oryzae*, on the other hand, achieved a faster average rate of 40 cm/minute which was equivalent to 576 m/day. These rates were not expected to be maintained in the field, for the ground surface conditions presented more obstacles than the laboratory floor or bench.

5.2.2. Description of Experimental Sites

A field, 2 hectares in size, was planted with Olympic wheat during the normal cereal growing season at Mortlock Experiment Station, situated 130 km to the north of Adelaide. No chemicals, except basic fertilizers, were applied to the crop. The crop was sampled periodically for the determination of the moisture content of the grain commencing at the "milk stage". Moisture was critical for a preliminary experiment (in the glasshouse) had shown that weevils may infest grain in the ears at 21% moisture. The sampling was achieved by walking along the diagonals of the plot and randomly picking 2 ears at 10 m intervals. The threshed grain was oven-dried and the grain moisture determined as the percentage of the wet weight.

When the grain moisture had dropped to 24% two replicated plots (Figure 5.2.1) each 80 x 80 m and separated from each other by a guard 10 m wide were marked out. A fence (galvanised iron strips banded with "Fluon") was erected in the centre of the guard and pitfall traps buried with their mouths level with the ground surface on either side of it. Each replicate comprised 8 quadrants and 8 annuli with the radius increasing by 5 m/annulus from the common release centre. A compass was used to find the direction and location of each quadrant.

The plant density in both replicates varied considerably. The western half of Replicate 1 had sparse, low wheat plants separated by small patches of bare ground, whereas the eastern half consisted of relatively tall and dense plants. In Replicate 2, which was situated 10 m away, plants were almost uniformly tall and dense except for the four outermost arcs between the two NE and SE where the plant cover was intermediate between the two extremes of Replicate 1. The ground surface was almost uniformly flat. With the advance of the hot and arid summer the ground developed cracks. At the time of release on December 15 1978, many cracks and crevices varying in width 1-10 mm had spread throughout the plot, especially on Replicate 2.

5.2.3 Trapping and Grain Sampling Techniques

Pitfall Trapping

Although pitfall traps have been shown to have many disadvantages (Southwood, 1966; Hayes, 1970), they can be used for studies of the occurrence and dispersal behaviour of apterous arthropods that walk about on the ground surface (Mitchell, *et al.* 1963; Greenslade, 1964, 1973; Southwood, 1966 and Den Boer, 1971). The dispersing organisms fall into the traps and are unable to escape.

The type of pitfall traps used in this investigation was polystyrene tubes, 3.5 cm in mouth diameter and 7.5 cm deep. The choice of this type of trap was based on simplicity and eas~~y~~e of operation.

There were 8 traps on each annulus (Figure 5.2.2), notwithstanding the increase in the size of successive concentric circles since their circumferences increased with the increase in radius from RP (release point). The position of the first trap on each annulus was selected at random by choosing a number from a table of random numbers. Otherwise each trap was located at a distance equivalent to 1/8 of the annulus's circumference. This technique has been used by Andrwartha (1971) to measure the rate of dispersal of snails *Helix aspersa* in the field.

From the statistian's point of view it was thought that no additional useful information could be obtained by putting more than one trap on each quadrant/annulus. However, the outermost annulus contained 5 traps per quadrant as an attempt to increase the probability of catching the weevils which might have by-passed all the traps in the inner annuli. This had the effect of making the probability of catching weevils on the 40 m annulus almost equal to that of catching them at 5 m concentric circle.

The traps were half filled with water while their mouths were coated with "Fluon" to prevent escape of the catches (Radinovsky and Krantz,1962) in case the water dried up through evaporation before the next round of replenishment.

The choice of water as the collecting liquid was made as a result of its superiority in catch efficiency over the other materials tested in a preliminary screening experiment. Weevil catches from traps containing alcohol-glycerol, formalin, liquid paraffin, water and blank (check) showed (Kruskal - Wallace H Test) significant differences in their catch efficiencies. The results ranked as follows: water > blank > formalin > alcohol-glycerol > liquid paraffin. In addition to effectiveness water was easily available, easy to work with and has not been shown to have attractant or repellent effects on invertebrates whereas some of the other preservatives have effects (Luff, 1968; Greenslade, 1971). Details of this experiment are shown in Appendix Table 5.1.

Ear sampling techniques

In studying the dispersal of insects in natural populations the ideal method, as reviewed by Southwood (1966) is to release marked insects at a point and observe their dispersal in space and time. Radioactive isotopes, fluorescent dusts, paints and dyes have been used for marking experimental cohorts (Dobzhansky and Wright, 1947; Griffin, 1952; Godwin, *et al.* 1957; Dobson, 1962; Doane, 1963 and Lamb, *et al.* 1971).

In this study there were no wild populations of *Sitophilus* in the field and precautions were taken to ensure that they were not taken there with equipment. Consequently it was unnecessary to mark the experimental cohorts. Nevertheless samples of grain in the ears were taken and examined for the presence of weevils to ensure that the crop was free from a resident weevil infestation and that any infestation that developed after release of experimental cohorts was directly attributable to the introduced test weevils which could only be distinguished by marking had these samples revealed the presence of a local weevil infestation. More samples were taken during the observation period after release as well as after the observation period to look for weevils in the ears. This was achieved by randomly (using a table of random numbers) selecting one station on each annulus (quadrant) and once selected that "Sampling Station" became permanent. Sample units, 70 ears (≡ 100 g shelled grain /"sampling station")were randomly picked at each sampling interval. Figure 5.2.2 is a diagramatic representation

Figure 5.2.2: Diagramatic representation of experimental sites.

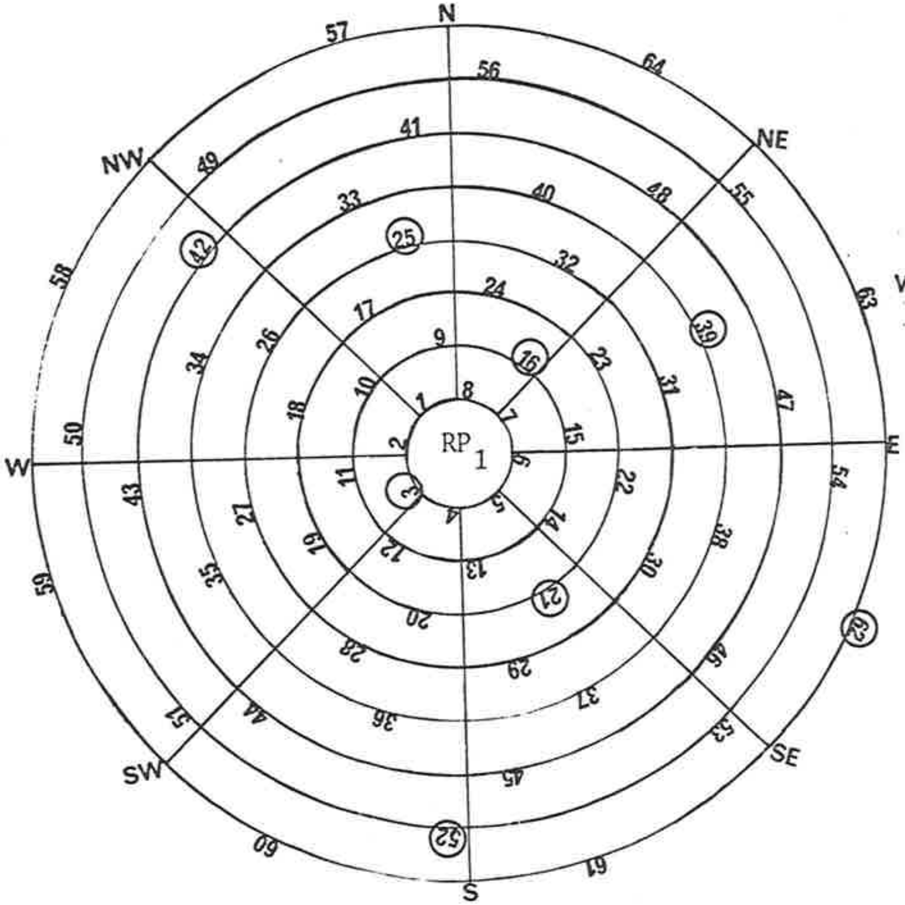
RP_1 - Release point on replicate 1

RP_2 - Release point on replicate 2

Open numerals - positions of pitfall traps

Closed numerals - positions of pitfall traps
and ear "sampling stations"

Letters - compass directions in relation to RP.


N
NE
E
SE
S
SW
W
NW
RP1
57
56
64
49
41
55
48
40
33
42
25
32
24
17
58
26
9
16
23
31
39
34
10
1
8
7
63
18
47
50
2
15
11
3
6
22
43
4
5
54
27
14
19
12
13
30
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20
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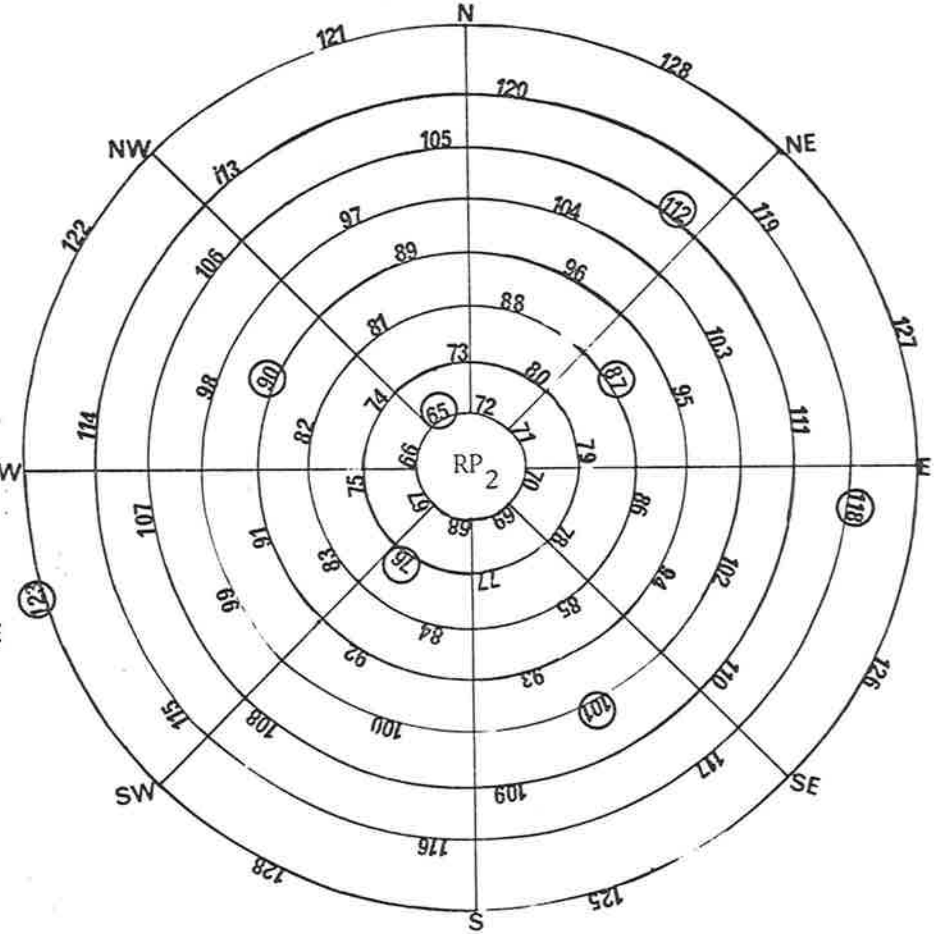
36
37
53
45
52
60
61


N
NE
E
SE
S
SW
W
NW
RP2
121
128
120
105
113
104
112
119
122
106
97
89
96
88
103
127
81
73
80
87
98
90
74
65
72
95
114
82
66
71
79
111
75
70
86
118
107
91
67
68
69
78
83
76
77
94
102
99
123
85
84
92
93
110
126
115
108
100
101
117
109
116
124
125

of the sites and sampling stations. Each sample was put into a sieve (4 mesh/cm) and vigorously shaken over a tray to dislodge weevils from the ears. Such sampled ears were then passed through a mini thresher which separated the grain from the ears and the grain was examined for symptoms of weevil damage. The moisture of the grain was determined on the standard moisture meter while the rest of the samples were incubated at 29°C and 70% R.H. to allow any pre-adult weevils present inside the grain to develop to emergence.

5.2.4 Experimental Cultures

Experimental cohorts were derived from stock cultures whose parents had originally come from resident infestations on farm stores. They were the 6th generation of such parents and had been reared side by side on Olympic at 29°C and 70% R.H.

When the moisture content of the grain in the field had dropped to 21%, 5,000 week-old adult beetles of each species were counted and immediately transported (in conditioned olympic wheat) to the experimental sites. Beetles of each species were carefully sieved out of the transport medium and released together at the common release centre. The only food available to them was the grains enclosed in the ears. Because of the substantial amount of work involved at the site the 1st release on Replicate 2 was made a week later than on Replicate 1. The 1st release on Replicate 1 was made on 15/12/78 shortly before dusk, on a warm overcast day with an air temperature of 24°C and a mild wind speed of 5 km/hr which was blowing in a N-Westerly direction. The 1st releases on Replicate 2 was made on 22/12/78 shortly before dusk, on a warm-hot dry day with an air temperature of 30°C and an average wind speed of 3.8 kg/hr. These meteorological data were provided by a thermohygrograph and an anemometer stationed at the site.

Sighting weevils without recapture enabled a series of observations to be made at intervals after release. Immediately after release observations were made at 0-4, 16 and 24 hr intervals and thereafter at 2 day intervals when the traps and their catches were collected and replaced by new ones. The initial observations were aimed at seeing how the beetles moved, where they went, whether they readily climbed the first plant encountered perhaps in search of food which was located in the plant ears, and the pattern of spread from the release point. The observations continued until the whole population had disappeared from the field, i.e. when no more weevils could be seen or recovered from the pitfall traps or wheat ears.

Further releases were made in mid-February in an attempt to improve on the recovery data and to try to obtain more information on the dispersal pattern. By then the physical conditions of the field had become more arid, with a grain moisture of 9% and daily maximum temperatures ranging from 35-46^{o}C.

The catches always comprised a great variety of arthropods in muddy water. Weevils were retrieved from the mixture by using the wet sieving technique which permitted mud and fine particles to drain away through a standard screen sieve of 12 mesh to the cm. This left a mixture consisting of weevils, other arthropods and solid materials and weevils could then be easily picked up with a pair of forceps, separated according to the species and their numbers recorded. In a few cases a microscope was used to confirm the species, especially those individuals which were partially mutilated.

5.3 Results and Discussions

5.3.1 Behaviour of weevils after release

The immediate reaction of individual weevils after release on the ground was a strong tendency to walk away from heaps of struggling weevils. Movement appeared to be in all directions, initially at least. Dispersing individuals did not seem to display a clear-cut tendency to climb the first plant encountered. The few which did climb wheat stems hid themselves in the folded leaves only to climb down again and resume irregular walking on the ground surface. Some entered and re-emerged from the cracks and crevices in the soil.

The environmental factors prevailing at the site at the time of release could be considered moderate in the light of what is known about the population dynamics of *Sitophilus* under laboratory conditions, and from my studies of the field biology of these species (Section 2). It would, therefore, appear unlikely that they would have had any significant effect on the behaviour of the weevils at that particular time. The wind speed would not have affected their dispersal behaviour for they never seemed to climb to the top of the plants from where they would have been carried down-wind, thus resulting in dispersal by wind drift. However these environmental conditions became more variable and hostile with the advance of the South Australian hot and arid summer weather conditions.

5.3.2. Recovery and Mortality

The numbers caught at the trapping stations on each annulus/ interval constituted a rough estimate of the number of weevils that had walked past that annulus into the next concentric circle and gave a measure of the average distance covered and hence the potentiality for spread of the infestation within or between fields of grain.

The observed recoveries for each interval showed (Figure 5.3.1) that the numbers dispersing reached a peak 6 days (*S.oryzae*) and 8 days (*S.granarius*) after release and thereafter the recovery rates progressively declined.

Table 5.3.2 shows the summary of recovery data partitioned into numbers caught/distance/compass direction and the total numbers recovered from each concentric circle over the entire period of observation after release. There was no significant difference in the trend with respect to the dispersal pattern of the two species on both replicates and consequently only results from Replicate 1 received further analysis and comments. Recovery data from Replicate 2 is shown in Appendix Table 5.3.3.

The total recovery of beetles over the entire period (21 days) of observation was 11.5% for *S.granarius* and 12.8% for *S.oryzae* on Replicate 1. This is lower than the recovery rate of 38% with marked white pine weevils (Godwin, *et al.* 1957), 27% with marked apterous cacao weevils (Lamb, *et al.* 1971). It is, however, a reasonable recovery and compares favourably with the results of Schoof, Siverley and Jenson (1952) who recovered 4.25% of marked *Musca domestica*, or Lindquist, Yates and Hoffman (1951) who recovered 4-14% of their marked flies, or Schoof & Severley (1954) who recovered 14% of their marked cockroaches.

Recovery rate depends upon (1) efficiency of the trap; (2) mortality, and (3) predation. Although the type of trap used in this experiment was not compared with other possible types for

Figure 5.3.1: Comparative catch rates of *S.granarius* (solid line) and *S.oryzae* (broken line) per observation interval after release.

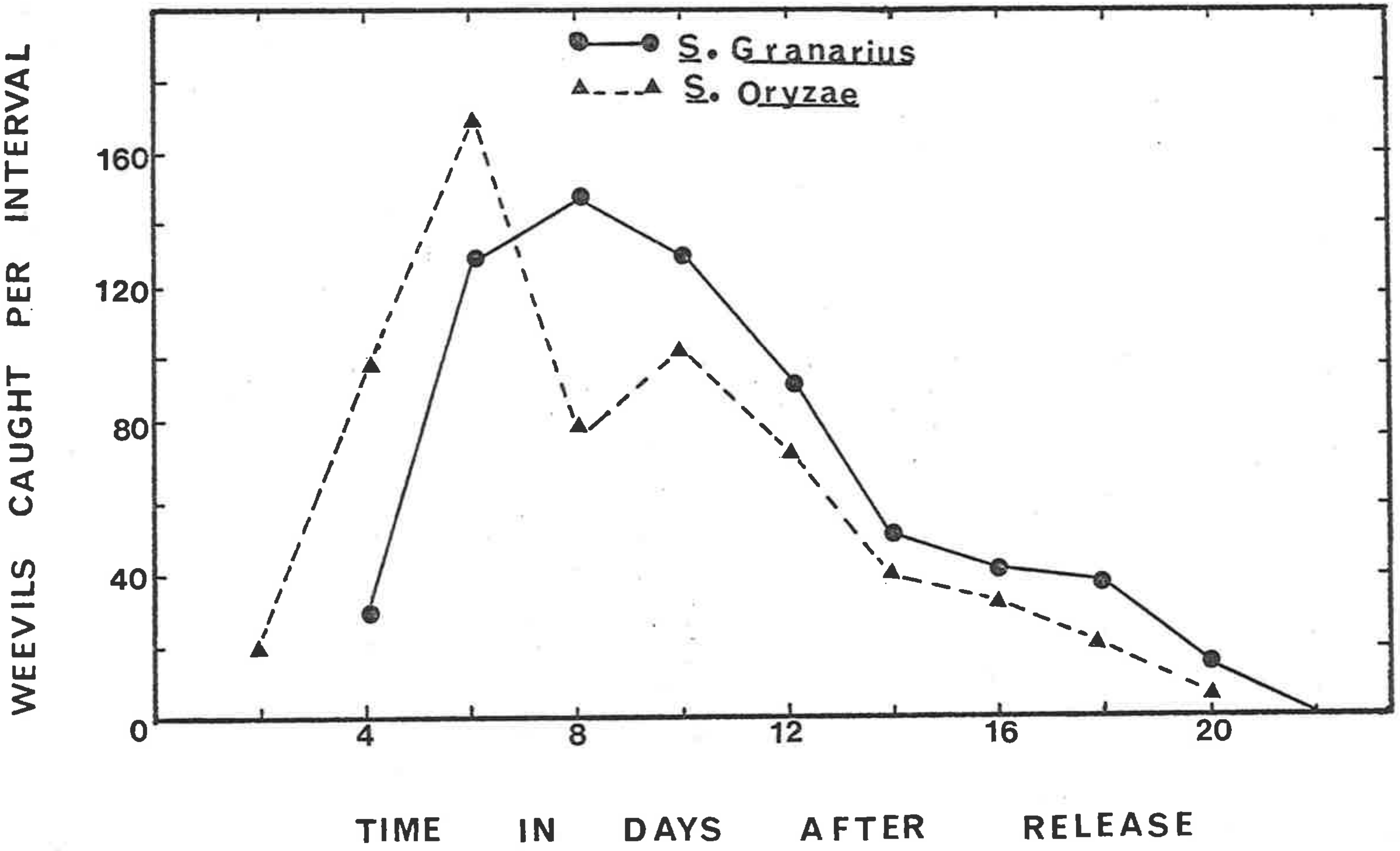

S. Granarius
S. Oryzae
WEEVILS CAUGHT PER INTERVAL
0
40
80
120
160
4
8
12
16
20
TIME IN DAYS AFTER RELEASE

Table 5.3.2: Catch Rates/Distance/Direction (Quadrant) for dispersing populations of *S.granarius* (A) and *S.oryzae* (B) on Replicate 1.

(A)

	Distance in meters from a common release point (RP)						
	RP	5	10	15	20	25	Total
Direction							
N		0	3	2	3	1	9
NW		62	28	23	8	2	123
W		53	40	25	2	4	124
SW		46	35	18	3	1	103
S		31	30	16	4	3	84
SE		40	4	12	5	0	61
E		24	10	17	0	0	54
NE		5	1	12	3	0	21
Total		261	151	125	28	11	575

No. originally released = 5,000
Recovery = 11.5%

(B)

	Distance in meters from common release point (RP)						
	RP	5	10	15	20	25	Total
Direction							
N		9	1	4	0	-	14
NW		78	50	13	0	-	141
W		87	24	7	5	-	123
SW		73	46	12	3	-	134
S		68	32	14	6	-	120
SE		28	2	8	1	-	39
E		67	14	11	-	-	72
NE		15	0	6	0	-	21
Total		405	169	53	15		642

No. originally released = 5,000
Recovery = 12.8%

efficiency the results obtained when it was used with water added to it (Section 5.2.3) appeared reasonably satisfactory for the purposes of this investigation. Pitfall catches should be proportional to trap diameters but it has also been shown that there is no loss of efficiency if small traps are used instead of large ones except for relatively large intertebrates (Luff, 1968; Greenslade and Greenslade, 1970).

During the course of the observations a number of dead weevils were sighted on the ground. It was suspected that this could have been due to desiccation as the daily maximum temperatures for mid-December-January and February averaged 36 and 38, respectively, with a range of 32-46°C. Starvation could have been another contributing factor since they were unable to feed on grain which remained protected in the ears. Unfed weevils die in about a week at 25°C (Singh & Wilbur, 1966; Coombs, *et al.* 1977) and about 3 weeks at variable temperatures (Back and Cotton, 1926). The last weevil taken from my experimental cohorts and kept without food under laboratory conditions died after 8 weeks. Probably, too, a number of them died and remained concealed in the cracks and crevices in the soil.

Another source of disappearance from the sites could have been predation and scavenging by ants. During observations a number of weevils, dead and alive, were seen being carried away by meat ants, *Iridomyrmex purpures* and scavenger ants, *Pheidole* spp. While in the process of sampling these ants for the determination of their relative abundance (in order to establish the likely rate of weevil predation by ants) other genera belonging to Myrmicinae, Ponerinae and Dorylinae were found to be represented in fairly large numbers. These are known to be carnivorous (Richards and Davies, 1977).

Laboratory experiments to verify predation of weevils by ants gave inconclusive results. Further investigations on ant predation of walking insects, including *Sitophilus*, would be a worthwhile effort. A possible experiment which might reveal the weevil toll due to predation, cracks and crevices would involve comparing catches from a site free from these factors with those from one where they are present while everything else remains similar. Nevertheless there are reasonable grounds to believe that a number of weevils disappeared from the site as a result of the activities of carnivorous and scavenging ants.

5.3.3 Rate of Dispersal and Spatial Distribution

The recovery data (Table 1) were analysed for both trends in the rate of dispersal with time and randomness of movement from RP.

The simplest model of mass dispersal from a point of release assumes that:

(1) The movement of individuals is uninfluenced by the presence or absence and activity of others around it;

(2) Movement is isotropic;

(3) Either individuals move by a constant distance per day or that their net displacement per day in relation to the position of RP is constant.

This is a two-dimensional random walk model which postulates a circular spatial distribution pattern, with a progressively increasing area in time. Assuming the presence of random dispersal by walking, movement would result in a spatial pattern which follows a circular bivariate normal distribution at any time after release (Skellam, 1951; Clark, 1962).

Since the movement of weevils varies with the physical components of the environment (Birch, 1946; Howe, 1951; Surtees, 1964), it is unlikely that individual weevils would have moved according to assumption (3). Assumption (1) could not be determined in this study.

Altogether 261 grain and 405 rice weevils out of the 5,000 beetles of each species originally released at RP were recovered in the traps on the innermost annulus. The numbers successively declined with the increase in radius from RP. The probability that a particular weevil would travel more than 25 m from RP in 21 days was about 1/1004, an extremely small figure.

Clearly the simple deterministic model that arthropods drift uniformly outward did not apply, since, if this were so I would have expected about 45 weevils of each species to be caught on the innermost annulus (by using the ratio of total trap diameters to total circumference).

The diffusion model described by Scotter, *et al.* (1971) appeared at first glance to be suitable. But since the value for D could not be determined in my study such a model proved to be inappropriate. Beside, these authors have also pointed out that irregularities (such as cracks and crevices, plant density (Section 5.2.2) and the effect of light) destroy the randomness of dispersal and therefore it would not be meaningful to define a diffusivity. A diffusion model with a variable velocity (preferably stochastic) and drift would be more satisfactory, however the development and testing of such a model lay beyond the scope of my thesis.

The catches from Replicate 1 (Table 5.3.2) were subjected to the X^2 test to see if there was homogeneity among traps at given distances from RP.

S.granarius

	Compass Direction from RP									
Distance from RP	N	NW	W	SW	S	SE	E	NE	X^2 values	P
5	0	62	53	46	31	40	24	5	105.43	**
10	3	28	40	35	30	4	10	1	94.446	**
15	2	23	25	18	16	12	17	12	56.096	**
20	3	8	2	3	4	5	0	0	14.285	**
25	1	2	4	1	3	0	0	0	11.545	NS

S.oryzae

5	9	78	87	73	68	28	67	15	150.197	**
10	1	50	24	46	32	2	14	0	134.591	**
15	4	13	7	12	14	8	11	6	22.99	**
20	0	0	5	3	6	1	0	0	22.866	**

**Differences among traps at given distances from RP were statistically significant with p = 0.05

NS - Not statistically significant with p = 0.05.

In the case of *S.granarius* recoveries from the 20 m and 25 m annuli yielded expected values less than 5; values which are too small to be meaningfully analysable by the normal X^2 test. Fisher's Exact Test, found useful for such small population distributions (Freeman and Halton, 1951; Southwood 1966), was therefore used and the results indicated homogeneity. ~~However heterogeneity was revealed when these (20 m pooled with 25 m values) were tested against those of the 15 m concentric circle using the X^2 test.~~

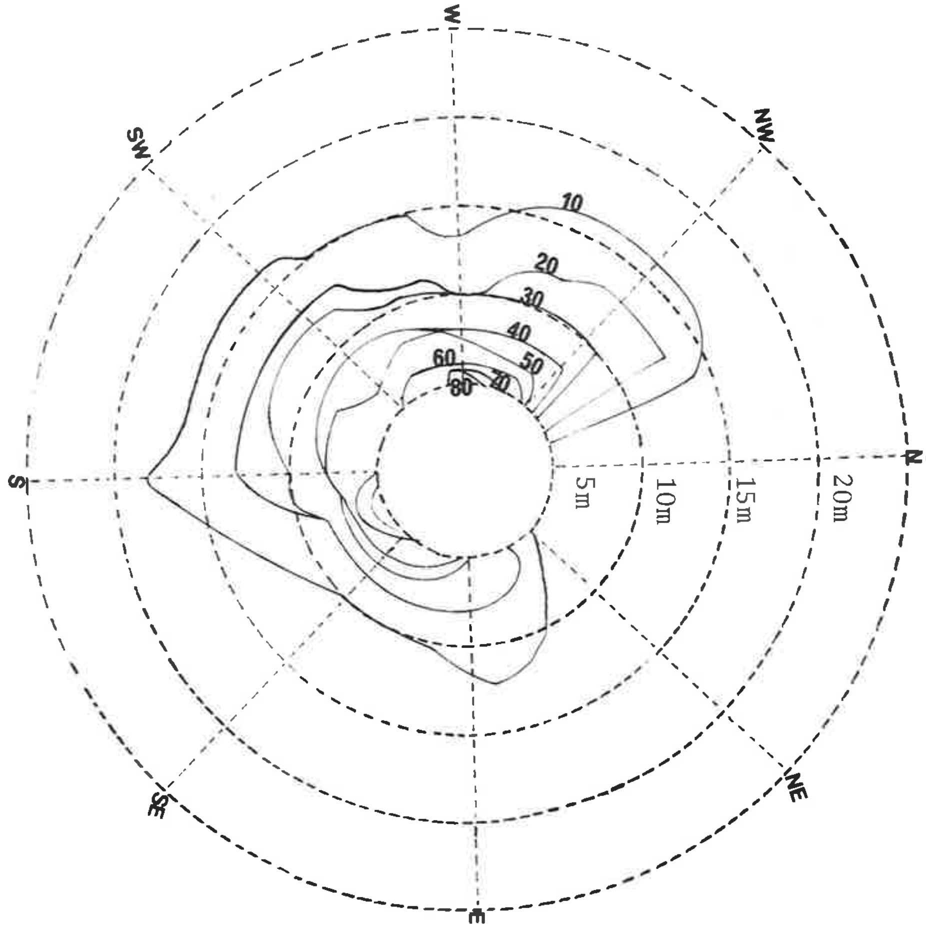
On the basis of the evidence of heterogeneity among traps at given distances from RP revealed by the X^2 test I concluded that spatial dispersal of both species was not uniform with respect to compass directions, but was consistently greater in certain directions, especially NW to S. Therefore the assumption of isotropic random dispersal behaviour for both species of *Sitophilus* was invalid.

Figure 5.3.3 is a simple contour map (linking areas of equal weevil catches) to show the overall spatial distribution of the dispersed weevils. Clearly there was a directional effect which tended to favour movement towards the NW-S directions with a minor axis towards the E for both species.

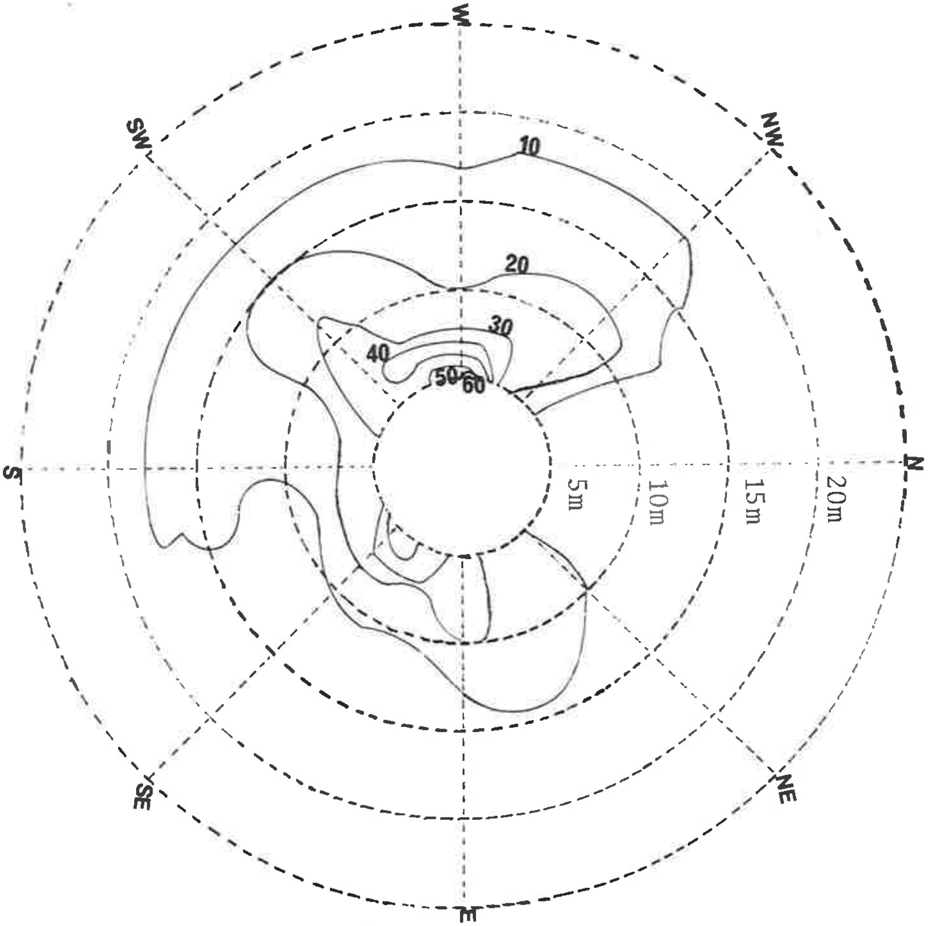
The reasons for the observed tendency of *Sitophilus* to drift into the western half of the field could not be fully explained with any certainty. It has been indicated that some insects are able to maintain constant directions during dispersal by orienting themselves towards the position of the sun in the sky (Andrewartha and Birch, 1954; Clark, 1962) while others will move in direct response to the plane of polarized light on overcast days (Wellington, *et al.* 1951; Wellington, 1955). However, the grain and rice weevils are known to be strongly negative phototropic (Dendy and Elkington, 1920; McLagan & Dunn, 1935) but Richards (1951) has also shown that *S.granarius* may temporarily become photopositive if mechanically disturbed. It has also been shown (Section 4.3) that *S.oryzae* consistently migrated in the direction of the shaded part of the shed and that under red light the migration of both species was random (Section 3.2.5). The dispersal behaviour of both species may therefore be expected to be negatively correlated with sunlight and the plane of polarized light in the field. The rows of the wheat plants were oriented in the SE-NW directions and since weevils shun light

Figure 5.3.3: Contour map showing areas of approximate equal weevil recoveries. Catches came from the same plot (RP_1) but results of each species have been presented separately for better comparison.

S.oryzae



S.granarius



I expected their dispersal activities to be positively correlated with the position of the shade cast by the standing plants. Releases had been made shortly before dusk and the following morning the sunlight as well as the shade of plants were directed in the E-W direction. This might have triggered weevil dispersal towards the shaded areas on the western side of the plants. As the sun rotated through an angle of 180^{o} to set in the west the shade moved from west to east. The weevils, whose numbers would have already been reduced through trapping during the initial light triggered western drift, might be expected to change their direction in response to that of the counter-clockwisely rotating shade, thus resulting in the observed NW-S quadrants spatial distributions with a minor axis in the E, where the shade would have been located at sunset. In the absence of the light factor during nights the dispersal patterns would be expected to become random (Wellington, 1955) but it was not possible to determine what effect this might have had on the observed dispersal patterns. During the day in hot weather, weevils normally sheltered in the shade of the plants. They were active only at night & on overcast days.

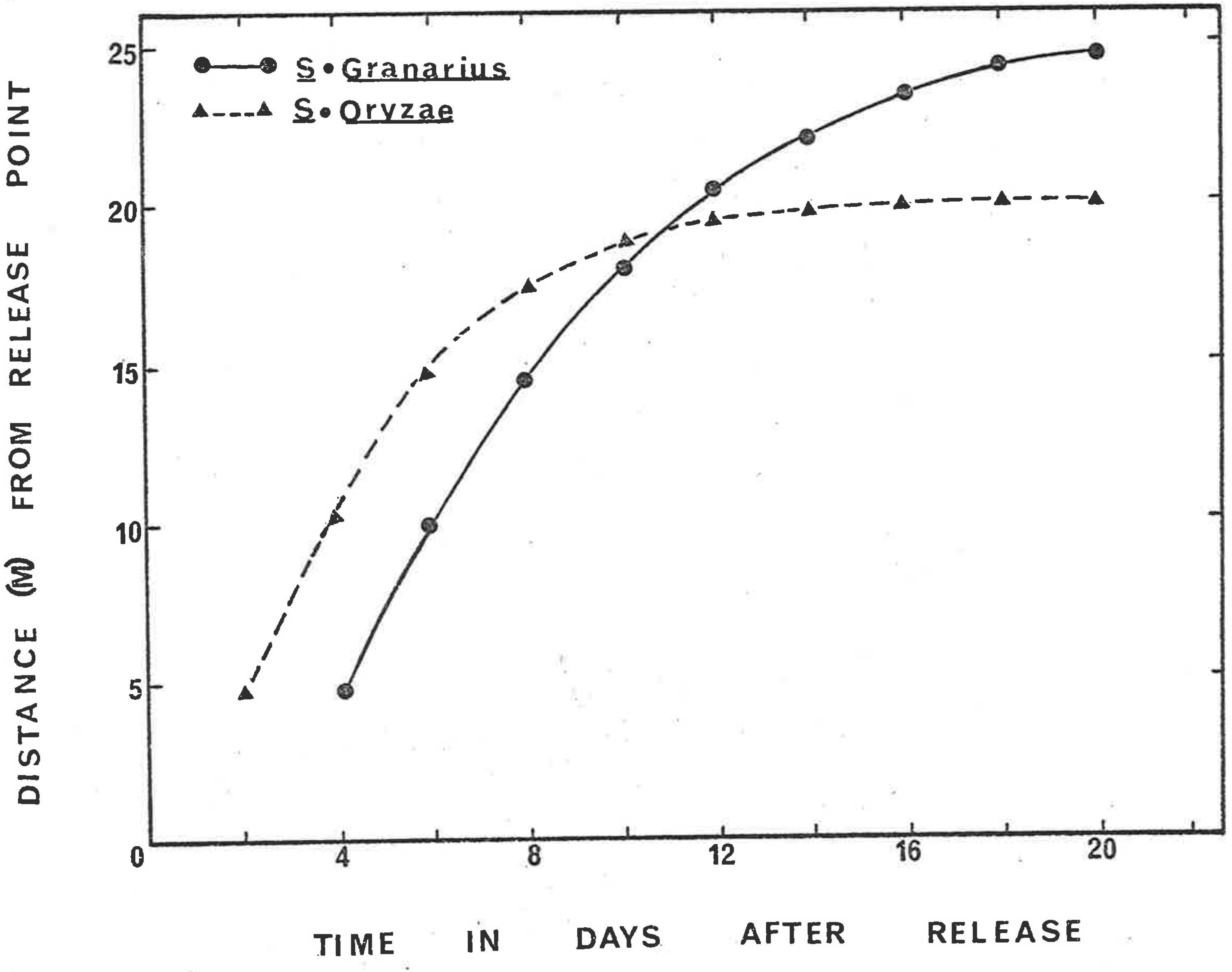
An experiment to verify the correlation between the position of the shade and the dispersal pattern would involve trapping weevil on a miniature plot of standing wheat plants in rows at short intervals as the sun rotates on a cloudless day.

From an economic point of view it is of interest to know the expected rate of spread of an infestation within a field or between neighbouring farm properties. One technique of estimating this is to plot the maximum distance moved per day by any individual for each observation. Figure 5.3.4 shows the maximum distance at which at least one individual was caught per observation over the 21 day observation period after release at RP. By dividing the maximum distance moved between two successive observations by the number of days between those

Figure 5.3.4: Maximum distance at which at least one individual was caught/interval over 21 days after release at a central release point (RP_1).

o——o *S.granarius*

Δ——Δ *S.oryzae*


S. Granarius
S. Oryzae
DISTANCE (M) FROM RELEASE POINT
TIME IN DAYS AFTER RELEASE
0
5
10
15
20
25
4
8
12
16
20

observations it can be shown that *S.oryzae* dispersed at 2.5 m/day during days 1-6 after which the rate progressively declined. *S.granarius* on the other hand, started dispersing at a lower rate of 1.25 m/day which steadily increased to reach a maximum rate of 2.5 m/day by the 10th day after release and thereafter its rate also progressively declined though at a comparatively lower rate than that of *S.oryzae*. The average dispersal rate for the entire period of observation (21 days) after release was 1.2 m/day for *S.granarius* and 0.9 m/day for *S.oryzae*.

Although *S.granarius* initially showed some reluctance to disperse it appears that dispersal rates of *Sitophilus* vary with time and the nature of the route. This would be in conformity with Clark's (1962) findings based on his studies of the dispersal behaviour of grasshoppers, especially those forms which disperse by "Unit jumps".

S.granarius is known to be less susceptible to adverse conditions of the environment than *S.oryzae*, a factor which may have contributed to its ability to achieve a greater maximum displacement distance than the latter. Handling and intense crowding of experimental batches may have had some selective effect on the tendency to move away from heaps of struggling weevils at the release point, this having been shown to be the case in some insects, including Curculionids (Dendy & Elkington, 1920; Clark, 1962; Greenslade, 1964). *S.oryzae* shows a higher degree of irritability from mechanical disturbance than *S.granarius*. This may account for the immediate dispersal at high rates shown by *S.oryzae* in this study.

Both species have shown a limited capacity for dispersal which is comparable with that of adult apterous cacao weevils, *Pantorhytes szentivanji* Mshl. which have the same mode of dispersal (walking). These weevils, though slightly bigger than *Sitophilus*, achieved a dispersal rate of 1.0 m/day in a close canopy and 0.6 m/day in open canopies (Lamb, *et al.* 1971). These small dispersal capacities shown by *Sitophilus* spp and other species confirm Den Boer's (1971) findings, based on his work with dimorphic carabid beetles, that in unwinged or brachypterous spp in which dispersal occurs only by walking the dispersal power generally will be poor. Nevertheless this limited power of dispersal appears to play a vital role in *Sitophilus* in enabling the species to maintain their populations over localized geographical areas. It enables the spread of weevils from an endemic infestation to fresh crop grain stored anywhere in the vicinity of that infestation focus.

5.3.4 Capacity for colonising grain in the ears

~~The grain in the ears sampled and treated by the methods~~ Grain samples, taken from the ears of a standing crop (5.2.3), ~~described above (Section 5.2.4) did not reveal any information~~ showed no evidence of weevil damage & produced no progeny. ~~about weevils entering, damaging or ovipositing in grains in the ears~~. Samples incubated at 30°C and 70% R.H. failed to yield any weevil progeny. The negative results contradicted the progeny emergences of caged weevils observed in the glasshouse observations ~~experiment~~. Some factors with a possible bearing on the weevils' inability to colonise a standing grain crop in the field are:

(1) The presence of a hard glume which completely covers the grain, thereby making the grain inaccessible to weevils, which would otherwise have to pierce the cover in order to reach the grains.

(2) The high daily maximum temperatures (range 32-46°C) recorded at the site had the effect of drastically drying the crop very quickly resulting in the grain moisture dropping from 24-8% in 14 days. The temperature and

(2) relative humidity data is shown in Appendix Table 5.3.5.

In the glasshouse observation the daily temperature and humidity factors were regulated and allowed to vary from 18-33°C and 65-90% R.H., respectively. These conditions, which are within the optimal range for the survival and reproduction of *Sitophilus* had the desirable effect of drying the crop slowly. Hence the crop and the glume remained soft and therefore vulnerable to weevil attack for a considerable time. Besides the plant leaves and tips touched the mesh on the walls of the cages thus providing a bridge upon which the weevils could walk in order to reach the grain ears.

Sitophilus is unable to cause damage to grain of 8% moisture for the purposes of feeding or oviposition (Birch, 1945; Howe,1965). Temperatures above 42°C are thought to be lethal to grain insect pests and a combination of this temperature and 8% moisture completely protects grain from attack by insect pests (Fletcher, 1911; Bailey, 1975). The findings of Rossiter (1970) who recorded positive progeny yields of *S.oryzae* in wheat samples collected from wheat fields in Queensland could not be confirmed in this field investigation. In South Australia, at least, *Sitophilus* showed no capacity for infesting grain in the ears of a standing crop in the field.

Conclusions

(1) This investigation has demonstrated that *Sitophilus* spp have small capacities for dispersal in the fields in S.Australia.

(2) Both species are unable to colonise a standing crop in the field under the S.Australian dry summer conditions and therefore they may be regarded as pests of stored grain with no ability to initiate a field infestation.

6 GENERAL DISCUSSION AND CONCLUSION

> "Entomologists concerned with practical problems (damage to stored grain by insects) have tended to consider ecology as 'academic' and have carried out trials with insecticides and made recommendations for their use without full awareness of the total effect in storage or warehouse environment"
>
> (Graham, 1970).

The investigations reported in this thesis were aimed at throwing light on the important aspects of the ecology and behaviour of grain weevils in their natural environment. The question of the origin of weevil infestations had been answered through extensive surveys of storage premises and harvesting equipment (Winterbottom, 1922; Freeman, 1948; Coombs and Freeman, 1955; McFarlane, 1968; Greening, 1969; Birks and McAliffe, 1973; Sinclair and White, 1979). Their findings led them to conclude that endemic populations in grain residues often served as sources of infestation for new-crop grain. Their sampling strategies enabled me to conduct my own survey of farm properties involved with the production and storage of grain in South Australia. The results (Section 1 and 4) confirmed the findings of the above workers. However, this study has ventured into the "unknown" by examining experimentally the whole process of inception and establishment of weevil infestations in nature.

Firstly, it was necessary to establish the expected rates of survival and productivity of small colonies of weevils in small grain accumulations under the environmental conditions on farms (Section 2). Secondly, since it is the colonies breeding in spillages which serve as sources of infestation for newly harvested grain, it was important to study their migratory and food searching behaviour (Sections 3 and 4).

Thirdly, it had been suggested (Rossiter, 1970) that weevils which damage grain in store might have their origins in field crops. In this respect it was of interest to know the capacity of *Sitophilus* spp to colonise a standing cereal crop in the field and the modes and expected rates of dispersal for either species (Section 5).

The general hypothesis underlying this study was that both species of *Sitophilus* may breed wherever sound grains accumulate and that individuals disperse in response to unfavourable conditions of their habitats. The different components of this hypothesis were isolated and tested individually (Section 2-5).

Earlier studies on these species under controlled laboratory conditions, notably by Eastham and McCully (1943); Richards (1944, 1947) and Birch (1945a-d, 1953) served as a benchmark upon which to test and compare the survivorship and reproductive potentials of my test strains of *Sitophilus* before commencing field experiments. Temperature and, though to a lesser extent, humidity played critical roles in the performances of the species under the fluctuating weather conditions of the field, as was the case in their studies. However, as expected, the actual results obtained (Section 2) were not comparable with theirs. A few young *S.granarius* were produced in winter (Section 2.3.3) when predictions based on the data of Eastham and McCully and Richards would have suggested none. *S.oryzae* completed development (egg-emergence of progeny) at temperatures below 15°C or 17°C indicated to be the lower developmental limits by Birch (1953) and Howe (1965), respectively. However, it failed to do so when the daily means varied from 7-10°C in mid-winter. Survivorship of experimental cohorts of both species remained high throughout winter in spite of the occasional fall of temperature to 0-3°C at all sites. However the two species differed significantly with respect to their response to very high temperatures. *S.oryzae* were annihilated at all sites when temperatures above 40°C were recorded in summer (Section 2.3.1 and Appendix Table 2.1). This may be an indication that the 40°C temperature it acclimated to (Gonen, 1977) was probably the upper limit before its thermal death point was reached. Although a few beetles of *S.granarius* survived temperatures above 40°C (40-46°C) reproduction ceased completely. Thus, in general, the striking interaction between low temperatures and aridity with respect to increased mortality of the immature stages (Birch, 1945d; 1953) would greatly reduce field populations of *Sitophilus*. More detailed explanations for these disparities have been presented in the discussion (Section 2.3) and tend to confirm Howe's (1963 and 1965b) postulations concerning the inappropriateness of the use of laboratory work to predict population growth in field studies.

It would appear, from the foregoing, that there are two periods (March - mid-May and mid-October - early December) per year during which small colonies of *Sitophilus* spp breeding in grain residues could multiply rapidly and possibly assume pest status. However, depending on the size of the grain accumulation and the density of the insects breeding in it high summer temperatures of 40°C and above may drastically reduce or even annihilate such colonies. The cold winters of South Australia will suppress population growth in spillages by inhibiting reproduction, (Appendix Table 2.1). Although adult beetles may survive the cold winters (Section 2.3.1, see also Evans, 1977c) the ageing factor may militate against effective reproduction by the end of the long cold season (mid-May - mid-October). The likelihood of this being the case is supported by the short mean longevities observed in Table 2.2 and the very low effective oviposition observed among the female parents which survived the winter period.

Although the studies cited above (Sections 1 and 5) had indicated that *S.oryzae* possesses normal functional wings this thesis has provided evidence (Section 5) which suggests that it does not use them for migration or dispersal. In fact it is ecologically indistinguishable from unwinged *S.granarius* with respect to behaviour and niches. Kiritani (1959) has reported that the Japanese strain of *S.oryzae* was undergoing a process of adaptation towards a life in granaries and in the process the relative length of its hind wings have become reduced. This has led to loss of the ability to fly. It may very well be that its South Australian counterpart is in this evolutionary phase. Further experimental work would be required to provide more information on the morphology and function of the wings of *S.oryzae*.

What is the ecological significance of crowding, in relation to migration and the 'epidemiology' of *Sitophilus* spp?. It has been shown (Section 3.2) that overcrowding appears to put a limit to further numerical increases in permanent habitats. A similar finding was reported by Park (1933) and McLagan and Dunn (1935) based on their work with *Tribolium confusum* and *S.oryzae*, respectively. The discussion presented in Section 3.2 highlights the results obtained and the possible explanation of the mechanics of this (growth limit) phenomenon. It has also been shown that there is a critical density (different for the two species) at which emigration becomes enhanced. This would occur long before there is any apparent shortage in the food supply. Crowding, therefore, leads to emigration which appears to have the consequences of stabilising conditions in the habitat and prolongs the life of the colony. This reduced overcrowding will create conditions favourable to the production of more migrants which could spread out and establish new colonies, thus extending the species range thereby increasing the chances of continued existence. That proportion of the population comprising non-migrants will always be faced with the prospects of a sudden crash to extinction due to ecological hazards or when all the food in the habitat becomes exhausted.

The emigration behaviour of *Sitophilus* may be describable by the "overflow" hypothesis (Den Boer, 1971; see also Gadgil, 1971; Dempster, 1975). The former has indicated that this kind of behaviour may be expected in permanent habitats where numerical increases often approach or exceed "carrying capacity". Although most of what is known about the general theory of insect migration (Dingle, 1972) is based largely on arthropods which disperse mainly by flight, the ecological stimuli, namely density, temperature, humidity, shortage of food supply, causing such migrations, are the same as for *Sitophilus*. Studies of the functional relationship between reproduction and migration have not been carried out for *S.oryzae*. It is likely that the findings of Surtees (1964), that migration of *S.granarius* is initially prereproductive (much as in the Oogenesis-Flight syndrome of Johnson, 1969) may also apply to *S.oryzae*. This could be so, especially since the two species have been shown to be ecologically indistinguishable (this study). Migration of *Sitophilus* spp. appears to parallel that of *Tribolium* spp. (Ziegler, 1977). The only difference would be that a colony of *T.castaneum* comprises migrants only, whereas the colonies of *Sitophilus* spp. and *T.confusum* comprise migrants and non-migrants.

The results obtained from the study on the capacity for dispersal of *Sitophilus* species in a field of ripe wheat have received a comprehensive discussion in Section 5. Suggestions or tentative conclusions have been made. Grain and rice weevils have been shown to have a small capacity for dispersal achieved through walking, and since they may be incapable of colonising a standing cereal crop, at least under the summer weather conditions of this experiment, they pose no threat to field crops. The scavenging of weevils by ants (see Section 5.3.2) would further reduce the prospects of walking weevils establishing viable colonies in the field. This limited dispersal, taken together with the migratory behaviour discussed above, will be an essential parameter in the dynamics of the species on a localised basis on individual farms. It will provide an escape mechanism which may lead individual beetles to bulks of grain in warehouses. If such individuals are able to mate, or the dispersing individuals included gravid females, breeding will occur providing the moisture of the grain is within the favourable range. The relative humidity of the air blowing over such grain bulks has also been shown to play a critical role (Section 3.4.3) in enabling weevil dispersers to locate a food supply.

Further experimental work will be required to find a model which could adequately describe the dispersal behaviour of weevils in the field. Another viable project could focus on the role of predatory ants on the destruction of dispersing populations of weevils. If it can be shown that predation is an important parameter in the lives of weevils in field situations, then the probability of weevils establishing colonies in the field will be further reduced. This will be the case since predatory ants are widely distributed in South Australia.

The ability of *Sitophilus* to achieve a wide geographical distribution is not severely hampered by the observed low dispersal capacities. Herford (1948) and Champ and Dyte (1976) have indicated that artificial dispersal achieved through man's grain trade practices ensures the widest possible distribution of these species. By this method weevils may be transported to distant places with the grain in which they are breeding or in infested empty containers or transport equipment. This would lead directly to problems of cross or residual infestation resulting from loading fresh grain into infested equipment.

The overall results of the investigations discussed in this thesis have relevance to certain general problems of pest control. The substitution of broad-spectrum insecticides for those with more selective action has created new problems of pest succession. Hall (1969) has shown that in the early 1950's *Sitophilus*, *Tribolium* and mite species of stored grain and cereal products were effectively controlled by the application of lindane. At the same time moth populations increased. In the 1960's when malathion came into use the same trend was observed. A possible explanation of this phenomenon advanced by Coombs and Woodroffe (1973) was that the insecticides, in addition to suppressing beetle populations, eliminated parasites of the moths, such as *Braconi hebetor*, *Proteneusid canescens*, anthocorid and reduviid bugs.

The practical conclusions to be drawn from the known facts of interaction and succession between pest species resulting from the application of insecticides, together with the problem of insecticide resistance (already discussed; Section 1) are that the discovery and implementation of non-chemical methods of control is both desirable and urgent. The quotation taken from Graham's work (this Section above) emphasized the need for clear understanding of the species ecology and behaviour under their natural environments. This thesis was aimed at achieving this.

What is the place of farm hygiene in the control of weevil infestations?. The various physical and hygienic methods currently in use have been reviewed in Section 1. Munro (1966), Greening (1969), Williams(1969) and Sinclair and White (1979) have all stressed the need for a high level of cleanliness of harvesting machinery and warehouses. They have advocated the physical removal and incineration of all grain residues followed by the application of light doses of a proven efficacious insecticide.

This study (Section 2) has shown that small quantities of grain, characteristic of spillages commonly found on most farms, are unlikely to support population growth of *Sitophilus* during the winter and summer seasons. The high temperatures and low humidities usually experienced in summer may kill all stages of grain weevils. It has also been shown (Section 2) that the mean monthly temperatures of 7-11.8°C for June - September (winter) inhibit effective reproduction. The existence of these two unfavourable environmental factors (cold and aridity) may help to keep insect numbers at sub-economic damage levels in small grain residues, at least. It is autumn and spring - early summer periods that may present problems of weevil outbreaks for the weather conditions may favour rapid population increases. Consequently the prophylatic measures to be sought must aim at preventing a population build-up during these two seasons.

~~The study of the structure of grain-flow in~~ In South Australia ~~(Section 1) has shown that~~ grain flows mainly from the farms directly to the Bulk-Handling Authorities where disinfestation and hygienic techniques are comparatively more strictly and efficiently applied than on individual farms. It has also been shown (Section 5) that weevil infestations are unlikely to establish themselves in standing crops in the fields and that individual weevils cannot travel far from a source of infestation. Taken together, therefore, it seems reasonable to believe that if inter-farm grain trade can be stopped in favour of direct trade between the farmer and the Bulk-Handling Authorities, the isolated farm weevil populations may be greatly reduced to sub-economic damage levels.

However, for farm hygiene to succeed as a prophylactic measure its integration with one or more existing techniques may be necessary. Levinson and Levinson (1979) have shown that the manipulation of stored product pests by mass-trapping them with sex and food attractants could serve a dual purpose, i.e., early signal of an impending infestation and the aggregation of such pests which could then be easily killed by limited application of an insecticide. The migratory and dispersal patterns observed in this study (Sections 3 and 4) could provide the background information required for the timing of such a control programme. Clearly an integrated control programme involving a vigorously applied hygienic technique, mass-trapping and, if necessary, a light application of an insecticide could markedly reduce weevil populations. ~~to levels where they no longer cause economic losses to grain~~.

The major conclusions arrived at in this study may now be brought together and summarised as follow:-

S.granarius and *S.oryzae* are pests solely of stored grain. Since they have a small capacity for dispersal the prospects of their exclusion from the list of serious pests of stored grain in South Australia are good, providing a more vigorously applied farm hygiene programme integrated with another suitably selected technique is strictly adhered to.

Appendix Table 2.1 (a-c): Temperature, grain moisture content and oviposition rates of *S.granarius* and *S.oryzae*.

(a) Site - Adelaide

Inspection dates	Temperature (^{o}C)		% grain moisture content	Mean No. of eggs/♀/Fortnight					
	Mean	Range		*S.granarius*			*S.oryzae*		
				(a)	(b)	(c)	(a)	(b)	(c)
15/11/77	21.2	(10-30)	14.1	1.5			12.9		
29/11/77	20.6	(12-34)	14.0	18.3			25.8		
13/12/77	23.5	(14-41)	12.4	27.0			30.7		
27/12/77	23.6	(12-42)	10.5	24.5			15.1		
10/ 1/78	24.7	(14-39)	9.8	21.1			11.4		
24/ 1/78	24.0	(14-43)	10.0	20.0			6.2		
7/ 2/78	22.6	(12-38)	10.0	16.9			*		
21/ 2/78	24.5	(14-41)	10.0	10.2			*		
7/ 3/78	22.2	(12-35)	9.5	8.0			*		
21/ 3/78	24.6	(15-43)	13.5	7.2	13.7		*	20.0	
3/ 4/78	16.6	(10-30)	13.0	5.4	21.2		*	14.8	
18/ 4/78	20.0	(10-31)	12.5	0.5	20.0		*	14.1	
2/ 5/78	16.6	(9-25)	12.5	0	17.8			13.0	
16/ 5/78	14.4	(7-25)	12.5		12.9			10.0	
30/ 5/78	12.6	(8-18)	13.0		8.7			5.3	
13/ 6/78	11.1	(6-17)	14.2		3.2			0	
27/ 6/78	10.4	(6-17)	14.5		2.1			0	
11/ 7/78	7.7	(3-16)	15.0		2.6			0	
25/ 7/78	9.6	(5-13)	16.6		2.2	0			0
8/ 8/78	10.1	(4-16)	16.8		2.0	1.9			0.5
22/ 8/78	8.7	(3-14)	17.0		1.6	2.4			2.1
5/ 9/78	11.8	(5-21)	16.4		0	9.0			7.2
19/ 9/78	11.7	(5-20)	15.8			11.7			10.0
3/10/78	13.7	(7-23)	14.4			15.0			10.0
17/10/78	16.1	(7-31)	13.6			15.8			6.0
31/10/78	18.1	(9-31)	13.4			12.0			5.1
14/11/78	14.3	(8-32)	13.5			10.3			4.0
28/11/78	20.7	(11-39)	13.2			10.0			3.5
12/12/78	18.5	(11-32)	13.0			8.6			2.1
26/12/78	19.8	(12-36)	11.0			2.5			1.0
9/ 1/79	26.4	(14-46)	9.1			0.2			0

(a) - New parental cohort (summer) season
(b) " " " (autumn) "
(c) " " " (winter) "

Appendix Table 2.1b:

(b) Site - Palmer

Inspection dates	Temperature (°C) Mean	Range	% grain moisture content	Mean No. of eggs/♀/Fortnight *S.granarius* (a)	(b)	(c)	*S.oryzae* (a)	(b)	(c)
14/11/77	15.3	(6-31)	13.8	1.0			8.0		
28/11/77	17.6	(7-31)	11.5	9.8			23.1		
12/12/77	21.0	(12-43)	9.0	28.5			31.0		
26/12/77	18.0	(10-33)	9.5	22.5			10.2		
9/ 1/78	18.8	(9-39)	9.8	21.1			7.8		
23/ 1/78	17.2	(11-32)	10.0	20.8			*		
6/ 2/78	17.8	(8-36)	10.0	17.0			*		
20/ 2/78	18.4	(10-28)	11.5	12.0			*		
6/ 3/78	17.3	(8-29)	10.2	10.8			*		
20/ 3/78	22.4	(10-38)	10.4	10.1	12.1			20.6	
3/ 4/78	14.2	(5-23)	11.2	10.7	25.2			30.0	
17/ 4/78	14.8	(7-29)	11.8	9.5	25.4			22.2	
1/ 5/78	15.5	(7-25)	12.2	8.7	20.1			15.7	
15/ 5/78	13.0	(3-26)	12.5	6.0	18.2			12.1	
29/ 5/78	11.6	(4-19)	18.4	0.8	11.8			6.0	
12/ 6/78	8.4	(3-15)	14.5	0.1	10.0			3.1	
26/ 6/78	7.0	(4-12)	15.0		6.1			1.1	
10/ 7/78	7.3	(2-14)	15.8		2.0			0	
24/ 7/78	8.4	(2-14)	16.8		1.8	0		0	0
7/ 8/78	8.1	(2-16)	16.5		0	0.8		0	0
21/ 8/78	6.7	(2-11)	15.0			1.8			0
4/ 9/78	7.8	(2-14)	14.2			2.0			0
18/ 9/78	8.8	(3-17)	13.9			8.1			2.3
2/10/78	10.9	(6-22)	14.0			11.0			7.1
16/10/78	13.6	(4-26)	14.0			12.1			8.4
30/10/78	14.0	(5-27)	11.5			11.6			6.8
13/11/78	15.0	(6-26)	11.5			10.8			4.6
27/11/78	15.0	(8-34)	10.2			10.7			3.3
11/12/78	14.6	(8-31)	10.2			9.9			2.2
25/12/78	14.8	(9-30)	10.0			7.2			0.4
8/ 1/79	19.8	(12-39)	9.0			6.8			0
22/ 1/79	18.9	(11-37)	8.5			5.0			*

(a) - New parental cohort (summer) season
(b) " " " (autumn) "
(c) " " " (winter) "

Appendix Table 2.1c:

(c) Site - Moorook

Inspection dates	Temperature (°C) Mean	Range	% grain moisture content	Mean No. of eggs/♀/Fortnight *S.granarius*			*S.oryzae*		
				(a)	(b)	(c)	(a)	(b)	(c)
14/11/77	18.0	(7-35)	13.8	3.5			9.3		
28/11/77	21.2	(8-35)	13.0	11.4			16.3		
12/12/77	22.2	(12-41)	10.0	18.0			20.8		
26/12/77	22.0	(9-38)	9.5	16.8			7.0		
9/ 1/78	19.0	(9-38)	8.0	14.0			*		
23/ 1/78	21.6	(9-40)	8.0	13.0			*		
6/ 2/78	21.7	(9038)	8.5	10.0			*		
20/ 2/78	20.4	(9-38)	8.5	6.0			*		
6/ 3/78	20.2	(9-36)	11.0	5.7			*		
20/ 3/78	21.8	(11-37)	13.0	5.0	11.0			19.5	
3/ 4/78	17.0	(7-30)	11.2	4.3	19.8			20.7	
17/ 4/78	14.8	(4-32)	12.0	0.2	18.7			15.0	
1/ 5/78	13.5	(5-27)	12.5	0	17.8			9.0	
15/ 5/78	12.2	(3-26)	12.8		11.1			6.4	
29/ 5/78	11.3	(4-20)	14.2		10.0			5.1	
12/ 6/78	9.6	(2-16)	15.8		7.2			1.6	
26/ 6/78	9.6	(3-18)	16.0		4.6			0.1	
10/ 7/78	7.3	(1-16)	15.6		2.9			0	
24/ 7/78	9.3	(0-15)	15.3		2.1	1.0			0
7/ 8/78	9.5	(3-20)	15.0		0.6	1.5			0.3
21/ 8/78	9.6	(1-20)	14.0		0.2	2.5			2.8
4/ 9/78	10.6	(2-24)	13.8		0	6.1			3.6
18/ 9/78	12.1	(1-26)	13.5			10.2			6.7
2/10/78	14.5	(6-28)	13.2			14.2			9.8
16/10/78	14.1	(2-30)	12.8			17.0			7.6
30/10/78	17.4	(7-33)	12.3			14.0			4.8
13/11/78	18.5	(7-30)	12.0			12.9			4.0
27/11/78	20.0	(9-36)	10.6			9.0			3.1
11/12/78	22.1	(8-39)	8.5			5.3			2.0
25/12/78	24.9	(11-45)	8.0			1.9			0.9
8/ 1/79	25.3	(14-40)	8.0			0.3			0
22/ 1/79	26.1	(16-46)	8.0			0			

(a) - New parental cohort (summer) season
(b) " " " (autumn) "
(c) " " " (winter) "

Appendix Table 5.1 (a&b): Numbers of Weevils/SPP caught in Pitfall Trap filled with various preservatives, water and blank (check).

(a) *S.granarius*

	Rep.	Day 1	Day 2	Day 3	Day 4	Day 5	Totals
Alcohol + Glycerol	1	8	7	1	7	0	96
	2	3 (15)	8 (25)	9 (18)	10 (23)	9 (15)	
	3	4	10	8	6	6	
Formalin	1	2	6	10	11	3	113
	2	10 (18)	13 (28)	7 (27)	7 (21)	9 (19)	
	3	6	9	10	3	7	
Blank	1	18	12	14	16	23	236
	2	22 (50)	17 (44)	18 (40)	25 (50)	11 (54)	
	3	10	15	8	9	20	
Paraffin Oil	1	0	2	0	0	5	18
	2	5 (5)	1 (3)	1 (2)	0 (0)	1 (8)	
	3	0	0	1	0	2	
Water	1	22	9	9	20	22	271
	2	12 (60)	20 (45)	29 (58)	16 (56)	19 (52)	
	3	26	16	20	20	11	
		.003	.007	.017	.002	.003	

Level of significance between treatments (P = 0.05).

(b) *S.oryzae*

Alcohol + Glycerol	1	15	9	11	6	10	(111)
	2	6 (32)	10 (27)	1 (15)	2 (19)	6 (17)	
	3	11	8	3	11	2	
Blank	1	8	23	10	8	19	(217)
	2	16 (38)	9 (49)	13 (38)	14 (43)	10 (49)	
	3	14	17	15	21	20	
Formalin	1	5	3	12	9	7	121
	2	13 (23)	5 (16)	5 (25)	12 (26)	15 (31)	
	3	5	8	8	5	9	
Paraffin Oil	1	1	3	4	4	2	32
	2	3 (5)	2 (10)	2 (8)	0 (4)	0 (3)	
	3	1	5	2	0	1	
Water	1	10	8	31	18	17	251
	2	24 (49)	14 (38)	18 (59)	20 (57)	11 (48)	
	3	15	16	10	19	20	
		0.022	0.003	0.025	0.006	0.003	

Level of significance between treatments (P = 0.05).

Traps were sunk and their mouths level with the surface of the arena. Trap positions were randomised. 150 adult weevils per species were released each day at the release centre. Few individuals were not recovered.

Appendix Table 5.3.3: Catch Rates/Distance/Direction for Dispersing populations of *S.granarius* (A) and *S.oryzae* (B) on Replicate 2.

(A)

	Distance in meters from a common release point (RP)						
	RP	5	10	15	20	25	Total
Direction							
N		8	6	5	0	0	19
NW		56	28	22	10	1	107
W		46	29	20	13	3	111
SW		33	37	18	8	0	96
S		16	0	7	0	2	25
SE		5	10	1	14	1	31
E		26	12	2	6	0	46
NE		12	5	0	2	0	19
Total		202	129	75	53	7	454
X^2 value		95.276	80.81	53.986	34.848	10.143	
		*	*	*	*	NS	

No. originally released = 5,000
Recovery = 9.1%

(B)

Direction							
N		16	10	3	0	-	29
NW		72	16	8	0	-	96
W		91	21	5	0	-	117
SW		69	6	9	0	-	84
S		27	7	5	0	-	40
SE		8	3	0	0	-	11
E		47	4	0	0	-	51
NE		1	2	0	0	-	3
Total		331	69	30	1		431
X^2 value		188.273	36.622	17.049	7.0		
		*	*	*	NS		

No. originally released = 5,000
Recovery = 8.6%

* Difference among traps at given distance from RP statistically significant with P = 0.05.

Appendix Table 5.5: Mean weekly Temperatures and Relative Humidities at Mortlock Experimental Plot.

Week commencing	Mean Weekly Temperature (°C) + range	Mean weekly RH (%) and Range
15/12/78 - 22/12/78	19 (12 - 32)	52 (82 - 18)
22/12/78 - 29/12/78	25 (15 - 42)	48 (75 - 22)
29/12/78 - 5/1/79	30 (18 - 46)	34 (69 - 10)
5/1/79 - 12/1/79	27 (18 - 38)	41 (70 - 13)
12/1/79 - 19/1/79	26 (15 - 42)	41 (80 - 10)
19/1/79 -- 26/1/79	26 (15 - 42)	33 (47 - 17)
26/1/79 -- 2/2/79	25 (16 - 41)	45 (74 - 16)
2/2/79 - 9/2/79	25 (15 - 41)	47 (77 - 17)
9/2/79 - 16/2/79	27 (13 - 40)	42 (75 - 12)

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FIELD AND LABORATORY STUDIES ON POPULATION DYNAMICS AND DISPERSAL OF GRAIN WEEVILS (COLEOPTERA : CURCULIONIDAE)

by

Shadrack Sariri Mlambo

Addendum to thesis

In answer to the examiners' criticisms I have made a number of minor changes and corrections to the thesis which have been inserted in the text. Major additions are given below.

Page 6, line 14

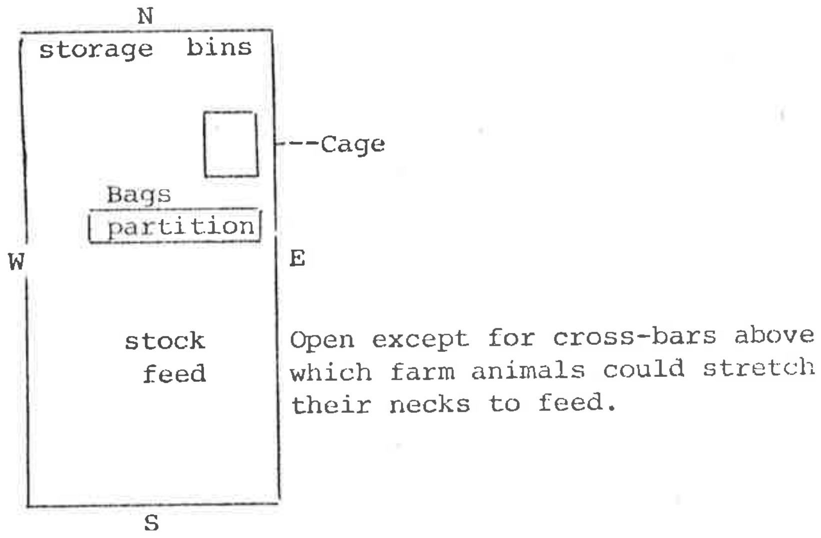
Control of stored grain pests by inert atmospheresis achieved by altering the normal atmospheric gases composition (78% nitrogen, 21% oxygen, 1% rare gases and 0.03% carbon dioxide) in an airtight filled grain store. Grain pests require oxygen in order to metabolise their food to produce energy for their survival, reproduction, developmental and mobile activities. This metabolic activity leads to the depletion of oxygen and an increase of CO_2. High concentrations of CO_2, N_2(and the corresponding reduced O_2 level) may be artificially pumped into the storage bulk. An O_2 concentration of less than 2% is lethal to all stages of stored grain pests. Protection of stored pests by this method compares favourably with other existing techniques. However complete airtightness of storage structures is vital for the success of this method. Any leakage of containers will allow the return to normal atmospheric gases composition.

Control of grain pests by means of refrigerated aeration has been found to be useful, especially in developed countries. The system comprises an air cooling system (ducts), means of forcing the chilled air (motor powered fans) through the grain and means of retaining the reduced subthreshold (below 15°C) temperatures throughout the grain bulk. The cooled environmental conditions of the grain bulk achieved by refrigerated aeration suppress insect population growth. Although this technique could be effective the refrigeration plant and its maintenance require high capital.

Page 16, line 27

At all the three sites the cages containing the experimental cultures sat on top of wooden blocks 45 cm above the floor. At Moorook the shed, about 12 m x 20 m was sheltered (asbestos wall) only on one side. The other unsheltered three sides consisted of steel pillars which supported the corrugated iron roof. The cage was located 4 m from the southern wall and 30 cm from the sheltered eastern wall; this being one of the two longer sides of the rectangular shaped shed. Five metres to the north-west of the cage were 6 bags of grain residue in which *S. oryzae* and other storage pests had been breeding for a number of years (see Section 4).

Palmer shed



The shed at Palmer was wholly walled (corrugated iron) on all sides except for the area shown in the diagram above. The cage was located 30 cm from the eastern wall and 60 cm from the partition (see diagram above). The farmer's grain storage bins were situated along the northern wall. Five bags of grain stood along the partition starting about 30 cm to the S-W of the cage. One of these bags containing barley was heavily infested with *S. granarius*.

The Adelaide shed was the smallest, being 5 m x 10 m in size. This was wholly walled (corrugated iron) on all sides and was kept closed all the time except when staff were storing or removing equipment. The cage was located at the N-W corner 30 cm from either the longer western wall or the shorter northern wall.

This field experiment, like that of McFarlane (1968), was designed simply to investigate the survivorship and productivity of grain weevils under highly fluctuating natural environmental conditions. Had mortality been a major objective then design of these experiments would have been different. It would have been necessary to replace all dead test weevils at each observation. More accurately, it would have been necessary to expose a new cohort of 120 beetles with more frequent observations. This would create parity in the experimental conditions and remove the possibility of death being due to old age. The nature of these experiments is such that if the data are subjected to correlation and regression analyses negative coefficients will result, thus suggesting that mortality increases as temperature decreases - the very opposite of what was observed during the hot arid summer season. The negative coefficients are caused by the fact that where high temperatures, 39°C and above, were recorded (see listing above) this was not always necessarily followed by death of a large number of test beetles. There does not seem to be a simple rationale for these deviations from the expected. It was more appropriate for Birch and other workers to correlate climate with mortality because they exposed constant numbers of beetle cohorts to different constant temperatures and humidities. In general it may be concluded that the detrimental effect of high temperatures on weevils, particularly S. oryzae, was apparent. However the type of data obtained may not be appropriately analysed by correlation and regression statistics.

The raw data for longevities, presented in summary form in Table 2.2, was lost by shippers during shipment of personal belongings from Australia to

Zimbabwe. The tests had been carried out and proper records of the life of each weevil had been taken.

Section 2.3.2

Statistical analysis of mean fecundities of Sitophilus spp. at Adelaide, Palmer and Moorook.

see Table 2.3, page 21

Table 2.3,A : Variate means for site x species x season. Site 1: Moorook, 2: Palmer, 3: Adelaide. Species 1: *S. granarius*, 2: *S. oryzae*. NOS: No. of observations (14-day periods); MNOE: Mean no. of eggs (per ♀, per 14-day period)

Site	Species	Season	NOS	MNOE
1	1	1	9	10.9
1	1	2	9	11.5
1	1	3	9	8.8
1	2	1	4	13.4
1	2	2	9	8.6
1	2	3	9	4.4
2	1	1	9	15.9
2	1	2	9	14.5
2	1	3	9	6.5
2	2	1	5	16.0
2	2	2	9	12.3
2	2	3	9	3.3
3	1	1	9	16.4
3	1	2	9	11.4
3	1	3	9	8.7
3	2	1	6	17.0
3	2	2	9	8.6
3	2	3	9	5.0

Table 2.3, B: Analysis of variance for mean number of eggs per ♀ per 14-day period (MNOE).

Source of Variation	d.f.	Sums of Squares	Mean Squares	F Ratio	Probability	
Site	2	99.792	49.896	1.00	0.37	
Species	1	274.102	274.102	5.52	0.02	*
Season	2	1871.294	935.647	18.85	0.001	*
Site x species	2	4.965	2.482	0.05		
Site x season	4	280.246	70.061	1.41	0.23	
Species x season	2	27.306	13.653	0.27		
Site x sp. x season	4	1.059	0.265	0.01		
Residual (Error)	132	6553.612	49.649			
Total corrected	149	9112.374				

To obtain the S.E. of the mean the following formula may be used:

$$\text{S.E. of the mean} = \sqrt{\frac{\text{Error mean square}}{\text{NOS}}}$$

Table 2.3, C: Mean number of eggs for species

Species	NOS	MNOE
1 *S. granarius*	81	11.6
2 *S. oryzae*	69	8.9
S.E. (d.f.75)		0.81

Table 2.3, D: Mean number of eggs for season.

	Season	NOS	MNOE
1	summer	42	14.8
2	autumn	54	11.1
3	winter	54	6.1
S.E. (d.f.50)			1.00

There was a significant difference between the two species. S. granarius produced a greater number of eggs. There was also a seasonal variation indicating that oviposition was most intense in summer, then autumn and rather sporadic winter. No significant difference existed between sites and also between the interactions (site x species, site x season, species x season and site x species x season). The above analysis has shown that the apparent lower mean numbers of eggs and progeny/lifespan (Table 2.4) at Moorook was not a true significant difference. It may be concluded, therefore, that the minor climatic differences between the three sites would not effect differences in the productivity of either species at any of the sites used in this project.

Page 30, last paragraph

The definition of emigrant is restricting. The type of apparatus (Plate 3.21), which gave the beetles only two choices - remaining in the habitat or departing - appears to justify that type of definition. Prus (1963) and Ziegler (1976, 1977) appear to have used the word "emigrant" in the same sense. "Tribolium beetles emigrated by climbing a pipe cleaner which extended from the surface of the flour upward through a short glass tube, and out into a collecting vial from which they could not return" (Ziegler 1977). Because this definition was restricting I therefore proceeded to carry out further experiments (3.3) in order to categorically characterise the emigrant as a true emigrant and not a passive follower of true emigrants.

Page 30, line 15 from bottom

Insert "90 cm from the western wall and stretching from the southern wall stood a steel frame with six shelves. The cultures were placed on the middle to the top shelves, the lowest of which was about the same level as the microclimate. This instrument sat on a chair 45 cm above the ground and 30 cm in from of the cultures and half way between the length of the shelves. The thermocouple wires stretched from this into the 3 "permanent" replicates of each treatment".

Page 42, 3 lines from bottom

Preliminary observations using water (about 60-65% RH) and a solution of potassium hydroxide (70% RH) as the substrates had shown no clear positive response to relative humidity alone. Although this observation was not rigorously pursued it appeared unlikely that the test beetles responded to unscented RH gradient. It was not intended to imply (p. 81, lines 11 to 13) that RH on its own would ordinarily induce a clear response among beetles but that humid air arising from grain of a suitable moisture content would do so.

Page 48, line 7 from top

Thermocouple wires probed into the bags of infested grain and the changes in temperature of the infestation could then be recorded on the graph. Maximum 2-hourly ambient and grain temperatures could be read against time directly from the thermohygrographs and thermocouple graphs, respectively. As stated on p. 30 a rise in temperature is correlated with intensive reproductive, and metabolic activities and that this is thought (Howe 1951) to trigger migration. As shown in Figure 4.1 an increase in temperature (ambient and grain) in summer resulted in large numbers of rice weevils migrating. Summer temperatures favour high reproductive and metabolic activities; hence temperature of the infestation would be expected to be higher than that of the ambient (Figure 4.1). The situation in winter is somehow reversed since the low day maximum temperatures have little effect on that of the huge bulks of grain. These will fall below those of the ambient and the reproductive activities are at their lowest levels. The change in temperature of the grain bulks lags behind that of the ambient (McFarlane 1968).

Page 51, paragraph 2

It has been stated that the dispersal pattern of *S. oryzae* was directional with 90% of the weevils dispersing towards the NE-SE compass directions. The raw data for these catches is no longer available but the monthly cumulated figures have been plotted in Figure 4.2 from which it is shown that weevil catches averaging more than 70 were taken within the NE directional zone. This is to be contrasted with catches averaging about 10 recovered in the NW-SW directional zones. That trend was repeated though with reduced values during the same period the following summer season. In April 1979 a total of 15 weevils (Figure 4.1) was recovered from traps. Thereafter no catches were recorded although sampling continued until July. When the grain culture was demolished in August 1979 no live weevil was found although *Tribolium* and other pests of crushed grain were present.

Page 55, 5.3.0: "Can *Sitophilus* breed in a standing cereal crop?"

The work reported in this subsection was aimed at throwing some light on the important question of the grain weevils' ability to colonise grain in the ears before harvest. Such preliminary information constituted part of the required background knowledge to the understanding of dispersal behaviour of the species in a field of ripe wheat.

The observations on colonisation were carried out in a glasshouse in which humidity and temperature varied from 65-90% and 18-33°C, respectively. Wheat plants (Olympic*8156) were grown in pots and the potted maturing plants were placed in cages made of steel frames and nylon mesh whose aperture was too small to permit escape by the smallest *Sitophilus*. The moisture content of the grain in the ears was determined periodically to time the release of test weevils. Two-day old weevils of either species were released on to the heads of the caged plants as follows:

25 ♂ + 25♀ at 45% grain moisture
25 ♂ + 25♀ at 35% " "
25 ♂ + 25♀ at 25% " "
25 ♂ + 25♀ at 20% " "
25 ♂ + 25♀ at 15% " "

These cultures were not replicated. Test weevils, dead or alive, were removed from the cages after 14 days. The grain was then harvested, shelled, examined for weevil damage symptoms, dried at 25°C and incubated at 30°C and 70% RH.

Infestation (damage symptoms and progeny yield) was positive at 20-15% RH. Although it was negative at 25% RH some infestation could have occurred at 22% RH as has been suggested by the data of Birch (1944b) and Richards (1947). Nevertheless progeny yields were 531 at 20% m.c. and 1605 at 15% m.c. for *S. oryzae* and 3 and 1 for *S. granarius* at the corresponding m.c. levels. This finding with regard to *S. oryzae* was in accord with that of Rossiter (1970) whose grain samples from field crops gave positive yields of this species. Yields of *S. granarius* came as a surprise for this species has never been recorded on field samples of grain before. Even then the four beetles harvested dead are a suspect result for no physical damage symptoms were apparent prior to incubation. However the four exit holes were seen.

They could not be remnants of the original parental cohorts for the shelled grain samples had been thoroughly checked before incubation.

Page 58, line 1

In the laboratory the walking speeds of either species were estimated by releasing adult weevils at a centre point of a laboratory floor and observing the average distance covered per minute. These rates were then expressed as cm/minute. The daily rates equivalents are therefore deleted as this is unnecessary.

Page 70, bottom

However heterogeneity has already been shown for the inner annuli (5, 10, 15 m) thus the directional bias in the dispersal behaviour of this species is still strongly suggested.

Following release of weevils the initial reaction was to disperse but they did not continue to do so for long. Instead they hid in cracks and crevices or sheltered themselves in the shade of the wheat plants. During these observations I was unable to detect any beetle in motion during daylight. However dispersal activities were detected at dusk and dawn. Although my searching activities with red light at night yielded negative results with respect to finding beetles in motion it is logical to believe that dispersal commenced at about sunset and continued throughout the night. This would coincide with cool weather conditions and darkness which has been shown (Dendy & Elkington 1920, McLagan & Dunn 1935) to be a vital factor in the normal activity rhythms of weevils.

Page 75, bottom of page

The conclusions reached in this section should not be over-emphasized for only 38 kg of wheat (for 2 releases on each of the two sites) was examined.

At harvest time in South Australia thousands of tons of grain are delivered to the Bulk Handling Authorities and so it is still possible to find some weevil presence in such large deliveries. Records at some of the storage silos I visited bore evidence to this. However such light infestations are infrequent and when they occur their origin may almost always be traceable to some residual infestation in the storage premises on some farms (as was the case at Palmer and Moorook - Section 2 above). In such cases the farmer would have used "contaminated" bins or trucks to carry the newly harvested grain from the fields to the storage depots.

The hot dry weather conditions prevailing during the harvest period in this study are by and large typical of the harvest periods in South Australia. There may be some difference in the degree of dryness but mid-December to February (harvest periods for winter wheat) are normally hot dry months.

Page 83, second paragraph, end of line 5

Add "but this would depend on the size and location of the spillage, for temperatures inside spillages larger than 100 g wheat (used in this study) may not vary as the ambient temperature".

Page 83, in support of last sentence on that page

During the course of this study I noticed that in certain localities such as Gawler and my experimental sites at Palmer and Moorook farmers in the neighbourhood would purchase left-over grain for stockfeed or bales of lucerne from these sites. The grain at Palmer carried an infestation of S. granarius while the bales of lucerne at Moorook were stored in a shed heavily infested with S. oryzae. This practice would obviously help to spread weevil infestations to farms previously uninfested.

Figure 3.3 Relation between density and emigration (Initial density 120 males and 120 females)