A STUDY OF POPULATION GROWTH OF

SITOPHILUS ORYZAE L. AND *SITOPHILUS GRANARIUS* L.

IN SINGLE AND MIXED CULTURE IN WHEAT AND RICE

A thesis presented in partial
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Dedicated to

My Mother and Father

SUMMARY

The oviposition rates, fecundity and lifespan of 100 0-7 day old adult S.oryzae and S.granarius were determined on wheat and rice at moisture levels of 12 and 16%. Oviposition rates for both species were low over a long period in rice and high over a shorter period in wheat (both 12 and 16% moisture levels). Overall S.oryzae was twice as fecund as S.granarius. Rice was the preferred seed species and 16% the most favourable moisture content. S.granarius lived longer than S.oryzae in rice but the reverse occurred in wheat.

In comparisons of developmental times from egg to adult the only significant differences were in 12% moisture content wheat where S.oryzae developed more rapidly than S.granarius and for S.granarius in wheat where development was more rapid at 16% than at 12% moisture content.

In single species cultures over three generations populations of both Sitophilus species reached greater levels in wheat than in rice. S.oryzae multiplied faster than S.granarius under all conditions. These results were consistent with data on oviposition rates and fecundity although S.granarius was slightly longer lived.

In mixed cultures populations of both Sitophilus species were reduced compared with single species cultures under the same conditions with the exception of S.granarius in 16% wheat where it performed better than in single species culture. Neither species was completely eliminated in mixed cultures but in 12% rice only very low numbers of S.granarius survived.

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CHAPTER ONE: GENERAL INTRODUCTION

Biological interactions between organisms which contend for the same resource, have been of interest to ecologists since the days of Darwin. Although this sort of association is evident for many animal-versus-animal and plant-versus-plant situations, one group which has received particular attention is the Class Insecta. Some insect species which attack stored grain and food products are especially convenient experimental animals for the investigation of some aspects of competition. Characteristics which enable insects inhabiting stored grain and grain products to become significant pests, include a short developmental period, resistance to dessication at all stages, a high reproductive rate and extended life span.

Of the many insects that have adapted themselves to a diet of dried vegetable material, a few are primary pests of grain in that they are able to bore into the sound kernels. Some major crops such as coconut, coffee and cotton, may be damaged by as many as 500-700 different species of insects but in general, the number of major insect pests of any crop is between 5 and 20.

The origin of insect pests of stored grain is uncertain. Undoubtedly, they formerly lived in the field, some of them breeding in supplies of seed that escaped the attention of birds and mammals, others feeding on the dried remains of plants, while still others perhaps bored into the roots, tubers and stems of plants (Cotton, 1941). Pest status is most commonly attained simply by an increase in numbers. The natural control of a population is upset by the practice of agriculture when the planted crop provides an unlimited food supply for a potential pest (Hill and Waller, 1982). The custom of storing seeds, roots, herbs and dried meats for food, adopted by man in early times, provided an easy living for the insects accidently brought in with these stores. Ideal conditions for breeding provided by such stores made it unnecessary for these insects to fly long distances in their search for suitable food. Evidence indicates that many of the insects that trouble grain stores today were prevalent in ancient times.

Cotton (1941) suggests that owing to the small size of many of the insects that attack stored grain and the ease with which they can conceal themselves in grain, many of them have been carried by commerce to all parts of the world and have become cosmopolitan in distribution. However, conditions in all parts of the world are not equally favourable for the development of all these insects, so that in some regions, where some species flourish, others are barely able to exist. Hill and Waller (1982) point out that seasonal increases in numbers usually result from changing climatic conditions (temperature, humidity and rainfall) and biological pressures (competition - both intra- and interspecific - parasitism and predation).

Many insect pests of stored grain are still to be found living in the field in regions where the climate is favourable. They breed in the seeds of many wild and cultivated plants and attack the growing grain as soon as it begins to ripen. In addition to rice weevil, other species particularly abundant in ripening corn are the Angoumois grain moth *Sitotroga cerealella* Oliv.; the pink corn worm *Pyroderces rileyi* Wals.; and the flour beetles of the genera *Tribolium* and *Gnathocerus*. In colder climatic conditions, a few species are able to survive the winter in the field. However, a certain number winter over in barns, granaries and elevators where they are protected from the cold. Additionally the congregation of large numbers of insects in stored grain or milled cereal products causes "heating" to occur, so that insects in these "hot spots" are not only protected from the cold but are able to remain actively breeding and feeding throughout the winter. Some of these overwintering insects later fly to the nearby fields and lay their eggs in or on the ripening grain.

Beetles classed as weevils are characterised by having the lower front part of the head prolonged into a more or less elongated beak or snout bearing the mouth parts at the tip. Several species of weevils attack stored grain, three of which are of primary importance as pests. The rice weevil, *Sitophilus oryzae* L. and *Sitophilus zeamais* Mots., which were originally found breeding in rice, prefer warm conditions and the granary weevil, *Sitophilus granarius* L., which can withstand lower temperatures. A fourth of the true-weevils is the broad-nosed grain weevil, Caulophilus latinasus Say. Unlike the rice and granary weevils, it is unable to feed on whole grain or seed that is dry and hard. It attacks cracked or damaged seed and grain before it is fully ripe and in addition may breed in acorns, avocado seed, sweet potatoes and roots of the dasheen.

Allied to the grain weevils are the grain borers and the most important of these is the lesser grain borer (Rhizopertha dominica F.). It is widespread in grain centres, attacking grain especially but also commonly found breeding in flour. Their larvae crawl actively, feeding on the flour produced by the boring of the beetles or boring directly into grains that have been slightly damaged.

One of the best known insect pests of stored grain in the United States is the cadelle, Tenebriodes mauritanicus L., which is thought to be a native of America. The large, fleshy larvae of this insect may burrow into woodwork of grain bins where they may remain until fresh grain is placed in the bins. The beetles feed upon grain, flour and milled products. Both larvae and beetles are found in accumulations of stock in elevator boots, flour conveyors and woodwork. This insect has a long life cycle of more than a year.

Several species of beetles that are not primary grain pests but feed on broken grain and grain dust, follow up the attack of the true grain beetles and complete the work of destruction. These include the flour beetles, Tribolium confusum J.du.V., and T.castaneum Hbst., each breeding in flour, foodstuffs and grain dust. Freeman (1960) in a survey of flour mills in many parts of the world has shown that in hot climates (both dry and damp), Tribolium confusum as well as T.castaneum occur but that in temperate climates T.castaneum is fairly uncommon.

Tribolium species are strong fliers which may account for their more frequent occurrence in farm stored grain. Developmental period from egg to adult may be short.

Other common beetles which are important pests of stored grain are Oryzaephilus surinamensis L. (saw-toothed grain beetle); the square-necked grain beetle (Cathartus quadricollis Guer); the foreign grain beetle (Ahasverus advena Waltl.); long-headed flour beetle

(Laetheticus oryzae Waterh.) and the broad-horned flour beetle (Gnathocerus cornutus Fab.). All attack stored grain and processed food in one way or another.

Moths which attack stored grain are usually encountered in hot, damp climates, e.g. Corcyra cephalonica Staint., but are usually absent from hot, dry climates. In temperate climates, only Ephestia kuehniella Zell. is important in unheated premises. The Indian meal moth (Plodia interpunctella Hbn.) also attacks stored grain and cereal products. This insect breeds freely in ear corn and flies to bins of shelled corn or other grains where larvae completely web over the surface by matting the grains together with silken threads.

Second only in importance to the rice and granary weevils as a pest of stored grain is the Angoumois grain moth, Sitotroga cerealella Oliv. It is known to lay eggs upon the ripening corn kernels and wheat heads in the field and spreads very rapidly while in storage.

Most other minor pests are scavengers, feeding upon the decaying grain and food products left behind by the other pests. They are rarely serious but are annoying and troublesome by their presence. Examples are the meal worms (larvae of comparatively large beetles belonging to the family Tenebrionidae).

Insects feeding or breeding in grains have an important advantage of being protected from adverse conditions such as very low or very high temperature, or humidity. They may also be protected from predators.

The behaviour and habits of stored grain insects are closely attuned to the moisture and temperature of their food media. For the most part the major stored grain pests are restricted to a narrow moisture band of between 11.5 and 14.5% grain moisture content. A moisture content of about 12.5% favours feeding and reproduction of most pests. Moistures above 14.5% permit the development of moulds and also of germination when temperatures are favourable. This results in heating, moulding and caking of the grain. A few insect species can utilise grain below 11.5% moisture, although their ability to do this varies with the species, the temperature and the physical condition of the food. Certain structural and physiological adaptations are essential for these storage insects to inhabit such a rigorous low-moisture environment. For example, their exoskeleton must largely prevent the loss of body moisture by evaporation.

The abundance of many insects in stored grain leads us to the question of how these pests live in the same niche and what happens if there are competitive interactions. From the literature, it is evident that many individual facets of the biology of the Sitophilus species (S.granarius and S.oryzae) have been well investigated. There is, however, a lack of information on the coexistence and competition between these species, although such work has been undertaken with species of other families and orders.

In Longstaff's review (1981) of the biology of Sitophilus species, it is apparent that only Birch (1953c) has attempted to investigate interactions between two Sitophilus species (S.oryzae and S.zeamais). He found that S.zeamais produced more progeny in maize but that on the other hand S.oryzae was more productive in wheat.

Coombs and Woodroffe (1963a) considered some interspecific relationships of Sitophilus granarius. They investigated the effect of S.granarius upon the mortality of eggs and newly-emerged larvae and pupae of Ptinus tectus Boield at 25^{o}C and 70% R.H. in wheat and in flour. The adults of S.granarius and Ptinus tectus appeared to cause mortality of P.tectus immatures but the effect was lower in flour than in wheat. This may have been due to Sitophilus adults often feeding on the germ of the kernel and thus damaging the seed coat. Although this provided shelter for P.tectus larvae it left them more susceptible to injury by Sitophilus. The overall effect was an increase in Sitophilus population and considerable decrease in P.tectus numbers. The authors imply that certain species depend on suitable structure of the food source.

Lefkovitch and Milnes (1963) studied interactions between the larval stages of Cryptolestes ferrugineus and C.turcicus and agreed with Birch (1953c) that relations between the two species were directly conditioned by habitat structure.

Ciesielska's study (1972) on population development of Calandra (Sitophilus) granaria L., Oryzaephilus surinamensis L. and Rhizopertha dominica F. in three two-species combinations was to determine the effect of interaction on the course of population development. Numbers of C.granaria in combination with O.surinamensis were almost twice as great as in single-species culture. C.granaria in this combination is a dominating species. When combined with Rhizopertha dominica F., however, the numbers of C.granaria were maintained at a very even and low level, far lower than when this species is combined with O.surinamensis, and lower than in single species culture. In the case of R.dominica, intensive development took place in combination with C.granaria. Similarly, in combination with O.surinamensis and R.dominica, the latter was again dominant. In these studies the total number of individuals obtained in two-species cultures was always greater than the number of individuals obtained in corresponding single-species cultures.

Ciesielska (1972) showed that when there is interaction between two species, depending on the combination, it either stimulates development in both species or inhibits development of one of the species, with simultaneous intensive development of the other. Ousting of a species takes place through inhibition of development, and not through a rise in its mortality.

In most experiments concerned with interspecific competition in closed laboratory populations, there is elimination of one species, the rate of elimination depending among other things, on the environmental conditions, the biology of the interacting species and on their genetic tendencies (Crombie, 1947; Park, 1948, 1954). It is necessary to find out when, during the development of a population, the competitive interaction is most severe and under what conditions coexistence is possible. In the granary weevil populations studied to date under favourable conditions, a number of interaction types have been identified:

(a) inhibition of the growth of the population of one species.

(b) inhibition of the growth of the populations of both species.

(c) stimulation of the growth of one population with a simultaneous inhibition of the growth of the other population (Ciesielska, 1972).

The latter is the most characteristic interspecific interaction of the competitive type.

In 1975, Ciesielska investigated in further detail, the mechanism of elimination of one species, aimed at establishing the stage of population growth at which the above processes are most intense. In the O.surinamensis and S.granarius combination, there was a lower fecundity for O.surinamensis. While S.granarius seems most affected by environmental factors (microclimate, amount of food), fecundity and development rate of O.surinamensis are controlled largely by the competitive action of S.granarius. Ciesielska concludes that competition between the two species begins during the initial period of population growth.

In 1982, Pontin published a book 'Competition and Coexistence of Species' in the broad sense. It has an indepth background on all aspects of competition and coexistence between various animal species. Relevant aspects will be discussed in relation to the present study in Chapter Five.

CHAPTER TWO: THE STUDY INSECTS

2.1 Taxonomic status

The genus Sitophilus belongs to the sub-family Calandrinae, family Curculionidae. The granary weevil Sitophilus granarius L. and the rice weevil Sitophilus oryzae L. and S.zeamais Mots. have achieved economically important pest status since they cause a huge loss of cereal seeds, the eggs being laid within grains and the larvae feeding on the endosperm.

Sitophilus oryzae is one of the most important pests of the majority of common cereals. This species not only occurs throughout the tropical and warm temperate areas of the world but also extends into certain cooler areas but is unsuccessful in regions with very high summer temperatures (Longstaff, 1981).

Sitophilus zeamais prefers moist and warm conditions in the more humid areas of the world (Longstaff, 1981).

Sitophilus granarius is a common pest of cereals in the cool temperate regions of the world, and is of particular importance in the Mediterranean region. In warmer regions it is usually restricted to regions of high altitude (Champ and Dyte, 1976). Charles (1976) suggested that the grain weevil originated from the Far East.

The three species are widespread in Europe and Great Britain (Motschulsky, 1855; Zacher, 1922; Howe, 1965); Kenya (McFarlane, 1968); India (Khan, 1949); Japan (Takahashi, 1928; Kiritani, 1965); South-East Asia (Santhoy and Morallo-Rejesus, 1975); the Mediterranean (Longstaff, 1981); North and Central U.S.A. (Cotton and Wilbur, 1974).

2.2 Nomenclature

Linnaeus (1758) first described the granary weevil

Sitophilus granarius, and called it Curculio granaria, then in 1763 described the rice weevil and named it Curculio oryza.

De Clairville and Schellenberg, in 1798, erected the genus Calendra to include granarius L. and oryzae L. The name had been mispelled Calandra and since then has been used in this form by many authors. In 1838, Schönherr restricted Calendra to the bill bugs and erected Sitophilus for oryzae L. (type) and granarius L. (Hemming, 1957).

Calandra has been placed on the official list of Rejected Generic Names by the International Commission on Zoological Nomenclature, and Sitophilus placed on the official List of Accepted Generic Names (Floyd and Newsom, 1959).

2.3 Morphology

Adult Sitophilus oryzae

Adult Sitophilus oryzae are brownish black in colour and have a dull appearance. Descriptions by Linnaeus (1763), Munro (1966), Khan (1949), Floyd and Newsome (1959) and Howe (1952) have been condensed as follows:

The head of S.oryzae is long and broad and is produced in front of the eyes to form a long rostrum, which is twice as long as the actual head. The rostrum is broad distally, narrow proximally and bent downwards slightly with mouth parts borne distally. The rostrum in the female is a little longer, thinner and more curved than in the male. The base of the head can be withdrawn into the thorax.

The ommatidia in the eyes are hexagonal. The eyes are broad anteriorly and narrow posteriorly. The antennae are as long as the rostrum, consisting of eight segments. Each antennae articulates like an elbow and is club-shaped at the tip.

The pronotum is densely punctured, the punctures being deep and round. Each puncture has a long scale in it (Khan, 1949).

Khan (1949) had also shown in detail the structures of the thorax and abdomen as well as the internal anatomy. He shows that the elytra are convex and sub-cylindrical and have four orange or iron-coloured patches. These patches vary: such as, oval in shape, kidney shaped or squarish. He also explains that in most females the two orange patches are joined by stripes of the same colour, which is a secondary sexual character. In this study, however, it was difficult to see these differences between sexes; some S.oryzae possessed elytra entirely orange-coloured, without spots.

The hind wings of S.oryzae are oblong in shape and truncated at the apex. Khan (1949) agrees with Grahame (1922) and Forbes (1922) in their studies on Coleopteran wing venation, that it is very complex in S.oryzae, especially the folding of the hind wing.

Adult Sitophilus granarius

Sitophilus granarius is also brownish black to black sometimes with a red tinge and is more shiny than S.oryzae. The general shape of the body is elongate and sub-cylindrical as described by Khan (1949). There are scales scattered over the body. The adult ranges from 3.2 to 4.8mm in length (Charles, 1976).

The head and its structures resemble that of S.oryzae. In S.granarius the similar sexual difference of the females having a longer, thinner and more curved rostrum is observed (Khan, 1949). The eye structure is identical to Sitophilus oryzae. Like that of S.oryzae, the antennae are elbowed and end in a distinct club (Munro, 1966).

In S.granarius the punctures on the prothorax are distinctly oval and fewer than in S.oryzae. The lines of punctures on the elytra are widely separated (Munro, 1966).

The hind wings in S.granarius have degenerated, which has affected the terga and the pleura. According to Khan (1949) the general shape and structure of the scutum, the absence of the posterior-suture dividing the scutellum into its sub-divisions and the obliteration of the prescutal lobes in S.granarius are some of its chief distinctive characters.

As S.granarius cannot fly, there appear to be some very obvious modifications; the elytra are fused (Khan, 1949). This has led to a great development of the rim of the 'subtural margin'. The hind wing venation differs markedly in the two species.

The median and the anals are absent in the venation of S.granarius. Owing to the degeneration of the wings in S.granarius, the axillaries have lost their function which has led to the fusion of the first and second axillary sclerites. The wing folding of S.granarius is quite simple and primary. The wing of S.granarius is much smaller than S.oryzae (Khan, 1949).

The distribution of bristles on the wing in S.granarius is quite different from S.oryzae, being restricted to the costa and the radius of the wing veins. There are also very few minute, clear, rounded bodies usually found in S.oryzae on the sub-costa, radius and cubitus of the wing veins, but these are restricted to only two on the cubitus of S.granarius (Khan, 1949).

There are no orange-coloured spots on the elytra of S.granarius.

The scarcity of bristles on the tarsal segments disables S.granarius in its progression on overhanging surfaces of glass. In general, S.granarius is slow in its normal movements and slower on glass. Khan (1949) elaborately discusses further minute differences.

2.4 Sex Differentiation

Apart from the difference in the structure of the rostrum in the females of each species, the shape of the lateral ventral surface of the female is a straight line, curved posteriorly in the male. Sitophilus oryzae females have stripes of orange colour joining two orange spots on the elytra.

2.5 Food Preferences

Sitophilus oryzae has been noted as one of the most important pests of post-harvest cereals in storage. It rarely attacks field crops since the conditions are unfavourable for its development. It has been found to attack split peas and hard grain products like pasta but can only breed in whole grains-cereals (Longstaff, 1981).

S.oryzae is capable of breaking open the toughest kernel and reproducing in large numbers. The species is often found in farm stores (Munro, 1966).

Birch (1953) and Floyd and Newsom (1959) made several observations on Sitophilus oryzae upon cereals, the former in Australia and the latter in U.S.A. They found that S.oyrzae is predominant on wheat and unpolished rice. Nevertheless, S.oryzae infested barley and maize as well. Kiritani (1965) pointed out from the experiment Kono (1960) unpublished, had conducted where wheat was relatively favourable for S.oryzae and rice was intermediate.

Baker and Mabie (1973a) reared larvae of S.granarius in a variety of media, whole wheat, whole corn and whole rice flour. Growth rates were highest on whole wheat.

The rate of feeding, however, depends on temperature, humidity, the type of food product and the pest density. Zacher (1927) and Steffan (1963) have done experiments that estimate the amount of grain Sitophilus granarius and S.oryzae consume daily over their entire life span. Golebiowska (1969) has done extensive research on feeding behaviour which he found was not consistent with the results of Steffan (1963).

Golebiowska (1969) observed that adults of S.oryzae fed at the same rate throughout the experiment. The weight of the food eaten by a larva during its development was 7.2 times greater than the weight of an adult S.oryzae; the food consumed daily by an adult was equal to 28% of its body weight.

Singh's (1981) results pertaining to the suitability of raw and milled rice show that brown rice (raw and parboiled) was very susceptible to S.oryzae attack.

Table 2.1: Showing the effect of wheat and maize on the size of adult Calandra oryzae (From Birch, 1946a)

Strain	Time	Wheat Total length.	Wheat Max.width mm	Maize Total length.	Maize Max.width mm
"Small"	7 gens	2.46	0.95	2.72	1.07
"Large"	7 gens	2.87	1.12	3.23	1.34
	1 gen.	-	-	3.30	1.40
"Atherton" (Large)	7 gens	2.84	1.20	-	-
	1 gen.	3.27	2.33	-	-

The insects from Atherton bred in wheat were reduced to the same size as the "large" strain bred in wheat and the large strain bred in maize became as large as the Atherton insects when bred in maize, thus confirming the identity in size of these two lots of insects. The small strain also increased in size when bred in maize but remained 0.2mm shorter than the large strain bred in wheat (significant difference = 0.1mm). This had previously been noticed by Kinoshita and Ishikura (1940) when S.oryzae they bred from rice became larger when bred in dried sweet potato.

Russell (1962) found that when mixtures of sorghum were offered to the test weevils, seed size (not hardness) was the determining factor, and that the larger seeds were preferred. The smaller seeds, however, had been completely hollowed out.

2.6 Life cycle

Richards (1947), Khan (1949), Howe (1952), Cotton and Wilbur (1974) and Longstaff (1981) have done extensive research on ovipositional behaviour and development of Sitophilus oryzae and S.granarius. Many of these authors also have studied the various factors which influence the oviposition rate of both these species.

Ewer (1945) dealt with the effect of grain size on oviposition and found that weevils laid eggs more rapidly in larger grains than smaller ones. Russell (1962) and Russell and Rink (1965) found that the relative hardness of the grain of various sorghum varieties was a dominant factor in affecting the oviposition rates. Russell (1968), however, also observed the effects of rice variety on oviposition. Relatively soft varieties received 2-6 times as many eggs as relatively hard varieties. In an attempt to establish the presence of resistance to rice weevils in rough rice, six American varieties were tested (Russell, 1968). The grain varieties varied from one another in iodine, amylose content, alkali value and grain type. An analysis of variance of the oviposition and number of days required for insects to emerge from grain indicated that effects of the varieties were highly significant ($p < 1\%$) for S.oryzae. There was no significant correlation found between these data and grain type (short, medium and long grains) or any other grain characteristics (iodine, etc.).

Reddy (1950) found that most eggs were laid, and the largest percentage hatched, at $30^{o}C$. Very few eggs were laid and none hatched at $13^{o}C$ or $35^{o}C$. Cole (1960), however, found $27^{o}C$ to be most appropriate for S.oryzae. The corresponding relative humidity was 84%. Maximum number of eggs were laid in 99% R.H. Relative humidity of 73% or less appeared to be distinctly unfavourable for egg-laying or hatching (Reddy, 1950).

Howe (1952) has done remarkable studies on temperature and relative humidity levels which affect oviposition rates. He found that the daily oviposition rate of S.oryzae at 25°C increases with relative humidity. The critical point is at about 60% relative humidity below which egg-laying declines rapidly and mortality is high. At 100% R.H., oviposition rate per female per day is 3.4 at 25°C.

More eggs are laid by females given more than one grain each. Daily egg output is reduced by grouping females or including males (Howe, 1952). In his 1965 paper Howe has tabulated the minimum temperature and humidity at which 53 pests of stored products can multiply effectively to pest status. This table explains the minimal and optimum conditions for each pest species.

Under favourable conditions, the female weevil chews a hole through the tough seed coat of the wheat grain and unpolished rice. It usually prepares a cavity in the endosperm in which to deposit an egg (Cotton and Wilbur, 1974). As the ovipositor is withdrawn, glands associated with it eject a white, gelatinous substance which fills the remainder of the oviposition hole not occupied by the egg. The naked eye can scarcely detect an infested kernel after the gelatinous plug has filled the cavity (Cotton and Wilbur, 1974). However, Frankenfeld (1948) and Sharifi and Mills (1971) have described effective methods to detect the plugs using vital stains and radiographic methods respectively.

Adult weevils feed on the endosperm of the grain kernel in the process of drilling cavities in which to lay their eggs. Unless the weevils have been disturbed, the eggs are usually deposited in all cavities that the adults drill into the kernels (Frankenfeld, 1948). If the populations are very large, however, many punctures that do not contain eggs may be found. This is because the female weevil had been disturbed while drilling the egg cavity and had not returned to deposit the egg (Frankenfeld, 1948). If the moisture content of the grain is comparatively low, i.e. 11% or less, the female weevil may drill a cavity but finding conditions unsuitable, will not deposit an egg. This explains the presence of a high percentage of egg-free punctures under such conditions.

The female weevil does not seal the cavity in the kernel unless she has deposited an egg. The total hatch is 85-90% of eggs laid. With moisture content and temperature conditions favourable, all larvae that hatch will complete their development (Frankenfeld, 1948).

According to Sharifi and Mills (1971), site of oviposition does not influence developmental period except that there is a relatively high mortality of first instar larvae which hatch in the centre of the germ. Sharifi and Mills (1971) also demonstrated the differences in oviposition site. Rice weevils deposited 1%, 44% and 55% of eggs in the germ, germ perimeter and endosperm respectively; while maize weevils deposited 21%, 37% and 42% respectively.

Quite often more than one egg may be laid in a single grain but it is rare for more than one larva to develop to maturity because of cannibalism. This view is shared by Khan (1949), Munro (1966), Howe (1972), Cotton and Wilbur (1974) and Longstaff (1981).

The description and finer details of the larval and pupal stages will be discussed in Chapter Four. However, there are four larval instars; all of which remain within the grain. Immediately upon hatching, the first larval instar feeds by burrowing through the tissues of the grain (Longstaff, 1981). Cotton and Wilbur (1974) describe how the newly hatched larva tunnels towards the centre of a wheat kernel until it reaches the crease; then tunnels back and forth along the crease. However, at times a newly hatched larva will feed just under the outer coat and make a pale scar that provides external evidence that a larva occupies the kernel. Rice weevils rarely cross the crease, so that in this case two weevil larvae may develop within a single wheat kernel provided their tunnels are on opposite sides of the crease.

At the end of the fourth instar the larva uses a mixture of frass and larval secretion to close off the end of the burrow to form a pupal cell. The larva greatly increases in size after each moult except the fourth. The width of the tunnel is indicative of the larval instar (Kirkpatrick and Wilbur, 1965). The larvae eat the endosperm and convert the starch into fatty tissue, which they store throughout their bodies (Cotton and Wilbur, 1974).

Durations of various life-stages have been well researched by Kirkpatrick and Wilbur (1965), Khan (1949) and Sharifi and Mills (1971a,b). This has also been investigated in this study (see Chapter Four).

By passing their developmental life inside a kernel, the larvae are protected from most natural enemies as well as from unfavourable environmental conditions such as extremes of temperature, and humidity. At the same time, they are surrounded by an abundance of nutritious endosperm (Cotton and Wilbur, 1974).

Under favourable conditions of moisture and temperature, rice weevils may complete their development from egg to adult in about four weeks (Cotton and Wilbur, 1974) to 36 days at 25°C (Khan, 1949). Sharifi and Mills (1971a,b) identified the different larval instars by measuring the widths of the tunnels. They also removed the larvae and measured their head capsules. Measuring the head capsules was also used by Khan (1949) and Soderstrom (1960).

The fourth instar larva assumes a prepupal form for a short period before it transforms into the pupa (Longstaff, 1981).

According to Khan (1947) the pupal stage of S.oryzae is shorter at high temperatures but high relative humidities prolong the period. Normally, the adults remain inside their kernels for a period of quiescence before chewing an escape hole through the seed coat and emerging (Cotton and Wilbur, 1974).

The preoviposition and incubation periods differ markedly in the two species at every temperature and humidity combination; whereas the larval instars are approximately of the same duration. The pupal periods of S.granarius are longer than those of S.oryzae, the total developmental period of S.granarius even at low temperatures (15^{O}C and 20^{O}C), is greater than that of S.oryzae (Khan, 1949).

Table 2.2 Specific differences between Sitophilus oryzae and S.granarius (Khan, 1949)

Feature	No.	Sitophilus oryzae	Sitophilus granarius
Colour	1	Brownish black to black and dull	Usually lighter and more shiny
	2	4 orange coloured spots on the elytra	No spots on the elytra
Punctures	3	Numerous on the body and are round	Fewer and are oval
Rostrum	4	Thick	Thinner
	5	At the base the lateral margins are almost straight	At the base, the lateral margins strongly converge internally
Labrum	6	Anterior margin not deeply notched	Anterior margin deeply notched
Mandible	7	Teeth moderately distinct and sharp	Teeth more distinct and sharper
Maxilla	8	Divided	Undivided
Eyes	9	Three times as long as broad	Six times as long as broad
Antenna	10	Club globose	Club ovate and slightly longer
Prothorax	11	Punctures numerous, deep and round	Punctures oval and shallow
	12	Nearly as long as broad	Slightly longer than broad
	13	Anterior margin less sinuate	Anterior margin more sinuate
	14	Bristles on the posterior margin simple and dentate	Bristles on the posterior margin simple
Mesothorax	15	Anterior margin of prescutum is not broad	Anterior margin of prescutum is broad

Feature	No.	Sitophilus oryzae	Sitophilus granarius
Mesothorax	16	Lateral margins converge gradually	Lateral margins are oblique
	17	Punctures numerous	Punctures fewer
Elytra	18	10 striae and 11 inter-spaces on the elytron	9 striae and 10 inter-spaces on the elytron, distinct and arched
Hind wings	19	Highly developed	Degenerate
	20	Wing venation complete	Wing venation incomplete
	21	Can fly	Cannot fly
Legs	22	Can move about on vertical glass surface	Cannot move about on vertical glass surface
Abdomen	23	Tergites thick, subsclero-tised and dark brown	Tergites thin, membranous and light brown
Propygidium male	24	Posterior margin narrow	Posterior margin broad
Pygidium	25	Twice as long as broad, narrow posteriorly	Nearly as broad as long, almost rectangular
Genitalia - median lobe	26	Long and uniform	Short and flattened apically
Median strut	27	Base constricted	Base not constricted
Tegmen	28	Shield-shaped with median piece between the lateral lobes bent upwards	Y-shaped without median piece. Lateral lobes bent downwards
Ejaculatory duct	29	Four sclerotised pieces at the apical margin	Two sclerotised pieces at the apical margin
	30	Denticles only	Denticles and papillae
Crop	31	Spines in the crop numerous	Few spines in the crop
Abdominal ganglion	32	Abdominal ganglion relatively smaller. The metathoracic and abdominal ganglia united and the two connectives are almost joined	Abdominal ganglion relatively larger. The metathoracic and abdominal ganglia distinct and connected by two well-separated connectives
Method of copulation	33	a) Male rides on the female, his proboscis touching the pronotum b) No second method observed	a) As in S.oryzae b) Abdomens touching and their heads facing in different directions
Larva			
Abdomen	34	First 3 abdominal segments divided into 3 transverse lobes	First 4 segments so divided
Pharyngeal rods	35	Fourteen in number	Twelve in number

Feature	No.	Sitophilus oryzae	Sitophilus granarius
Pupa	36	Hind legs partially covered by metathoracic wings and elytra	Hind legs covered by elytra only
	37	The posterior margin of the propygidium in the female is narrow	The posterior margin of the propygidium in the female is broad

CHAPTER THREE: RATE OF EGG LAYING, TOTAL FECUNDITY AND LIFE SPAN OF SITOPHILUS ORYZAE AND S.GRANARIUS

3.1 Introduction

Once insect infestation of grain has taken place, the rate at which it develops depends on the insect population density and on the extent to which the conditions favour multiplication. Factors determining multiplication rate include length of the period before a female begins laying eggs, rate of oviposition, rate of development at juvenile stages and the duration of adult reproductive life. These factors, in turn are influenced by environmental conditions (Eastham and McCully, 1943). Food condition is another factor, as adult weevils feed preparatory to oviposition (usually on the same grain in which they oviposit).

The biology of Sitophilus species, especially S.oryzae and S.granarius, has intrigued ecologists ever since Linnaeus first named them. Such interest increased as Sitophilus species achieved pest status in grain storage. Longstaff (1981) gives an excellent review of literature of the biology of these species.

The rate of oviposition has been found to be influenced by several factors. The extensive study of Eastham and McCully (1943) on oviposition responses, over a range of temperatures and relative humidities, showed that relative humidity has the most marked effect within the range 40% to 80% R.H. Temperature had less influence. Richards (1944) compared oviposition performance of S.oryzae at a single temperature, under a variety of humidities. His results also show that an increase in relative humidity increases the rate of oviposition. He also discovered that the rate of oviposition was far from uniform.

At 25.5^{o}C and 70% R.H., (Birch, 1945c, d) found that females of S.oryzae laid a total of about 850 eggs at an average of 9 per day. He showed that optimal environmental conditions for egg laying were between 25^{O}C and 29^{O}C at 70% relative humidity. However, Eastham and McCully (1943) obtained only a total number of 135 eggs per weevil at 25^{O}C and 70% R.H. Howe (1952) determined the total oviposition for 90 female S.oryzae in single wheat grains at 25^{O}C and 70% R.H. He also subjected them to several moisture levels, one of which was 12% and another 16%. At 12% moisture content, total number of eggs laid per female was 66 and at 16%, 112. While results of Anderson (1963) comply with those of Birch, those of Evans (1977a, b) and Hardman (1978) are different and show much lower values for total productivity at 70% R.H. Golebiowska (1969) showed that at 28^{O}C and 75% R.H., an average of 120 new adults emerged from eggs laid by 100 adult Sitophilus oryzae, i.e. an average of 2.4 eggs per day.

Food can also influence oviposition rate. Khare and Agrawal (1963) used two food types (wheat and maize) at three temperatures and four relative humidities. The Sitophilus species laid more eggs in maize than in wheat under all conditions. Ewer (1945) discovered that S.granarius females laid more eggs in large wheat grains than in small ones. According to Kiritani (1965) S.oryzae gave rise to a greater number of progeny than S.zeamais on wheat and on rice.

Wilbur and Mills (1972) have determined grain moistures which are favourable to grain weevils. On grain of 12 to 14% moisture, there was vigorous egg laying, but above 14% there was extensive mould growth as well as germination of the seeds. S.granarius can reproduce in grain of 10% moisture and can survive on a minimum of 9% moisture (Wilbur and Mills, 1972).

Other factors which influence rate of oviposition include slight crowding which may stimulate rate of oviposition and intense crowding which depresses oviposition rate (Crombie, 1942). The depressed rate is caused by 'jostling' or contacts between individuals, reduction in the amount of food available to individuals and 'conditioning' of the medium by the accumulation of various metabolic waste products. Overcrowded or underfed larvae may in turn produce stunted and less fecund adults (Mackerras, 1933; Wielding, 1928), while in the adult crowding may influence feeding, rest, copulation or oviposition itself.

The eggs are usually laid singly in two favourite sites on the seed; that is, in wheat, in two narrow bands, one band margining the germ and the other at the brush end.

The preoviposition period of the two Sitophilus species differs at various temperature and humidity combinations, low temperatures and humidities prolonging the period. This is also the case at high temperatures and humidities above the optimum. The preoviposition period is specially sensitive to humidity. Cotton (1920) found the duration of the preoviposition period of S.oryzae to be from 7 to 94 days during the warmer months of the year and of S.granarius to be 6 to 148 days. Mathlein (1938) gives the preoviposition period for S.oryzae at 25^{O}C as 4 days and for S.granarius at 25^{O}C, 5 days. Anderson (1938) records the shortest preoviposition period for S.granarius at 26^{O}C as 10-11 days. This period is longer in S.granarius than in S.oryzae at all temperatures and relative humidities (Khan, 1949).

Weevils live longer at low than high temperatures. Those temperatures which are conducive to an increased oviposition rate are in general those which lead to shorter life. At 25^{O}C to 27.5^{O}C, the majority of weevils continue to lay eggs until they die (Eastham and McCully, 1943).

Back and Cotton (1926) found that the average life span of adults under unspecified laboratory conditions was about 210 days. Lavrekhin (1937) states that at 25-27^{O}C female weevils lived for about 130 days. Cotton (1941) found that adult S.oryzae live for an average of 4-5 months (120-150 days) laying about 300-400 eggs in total, and S.granarius living for a longer period than S.oryzae (average of 7-8 months). Under favourable conditions (25^{O}C, 70% R.H.), Richards (1947) showed 50% mortality in mass cultures of Sitophilus species after 22 weeks. Mean adult longevity at the above conditions was 175 days for isolated Sitophilus females and slightly less in mass cultures. Rapid death of the experimental S.granarius populations was surprising to Coombs and Woodroffe (1963c). They found that longevity on wheat was slightly shorter than was found in cultures by Richards (1947).

The present study on the rate of egg laying, total fecundity and life span of both Sitophilus species attempted to establish these parameters for my populations of these species under the chosen experimental conditions, temperature and relative humidity being constant at 25°C and 70% R.H.

3.2 Materials and methods

3.2.1 Insects

Fresh colonies of Sitophilus oryzae and Sitophilus granarius were started by placing infested grain with new grain. The cultures were maintained at a constant 30^{O}C in a Warren Sherer germinator.

The weevils were regularly sieved from the grain and fresh grain was infested, while previously infested grain was returned to 30^{O}C until more adults emerged. Adult weevils aged 0-7 days were used in the experiments.

One hundred active adult weevils, 0-7 days old, were used in each treatment. It was impossible to sex the animals, and it was assumed that the sex ratio was 1:1.

3.2.2 Grain

Two types of grain were used in this study, whole wheat and unpolished rice, purchased from health stores in Palmerston North to avoid contamination by insecticides. The grains were carefully observed for pre-contamination and then, as an added precaution, heat treated at 80^{O}C for 9 hours. Grain was randomly sampled using the sampling tray prescribed by ISTA. This device divides the grain as it flows through it and in turn mixes the grain thoroughly and evenly.

The initial grain moisture contents (SMC) were 12% for wheat and 16% for rice.

The heat treatment of grain reduced the moisture content of wheat to 7.5% and the rice to 4.1%. The SMC was calculated according to 1976 ISTA procedures, i.e. ground and oven-dried at 130^{O}C for two hours. A grinding mill was used. Care was taken not to heat the grain as it was being ground.

The moisture content of rice and wheat after heat sterilisation had to be increased to the two levels required for the experiment. This was accomplished by keeping the grain at $5^{o}C$ and gradually adding water until the required moisture level was reached.

3.2.3 Determining oviposition

Several techniques of examining grains for eggs were evaluated. Cultures of 100 weevils were kept in plastic jars with airtight screw lids. Each jar contained 400 grains. The grain was sampled regularly and examined for eggs.

The initial method of examination (soaking in alcohol and examining slices of grain beneath a stereo microscope) was discarded as being inefficient. A second method, using vital stains to detect egg plugs was tried. This involved mixing acid Fuchsin powder with acetic acid and allowing the seeds (which had been presoaked in water for five minutes) to soak in the mixture for two to five minutes. The grain was then rinsed under cold running water, dried lightly on tissue and viewed under the dissection microscope.

While the method was successful using wheat, rice grains rejected the stain and the method was abandoned. Oviposition was thus assessed indirectly from the number of adults which eventually emerged and the results gave minimal egg-laying rates only.

3.2.4 The experimental design

One hundred newly emerged adults of Sitophilus granarius were placed with 400 grains of unpolished rice or whole wheat at 12% SMC. The same number was placed with 400 grains of unpolished rice or whole wheat at 16% SMC. Each treatment had 4 replicates.

Similar cultures (but with only three replicates) were set up using 100 newly emerged Sitophilus oryzae. The reduced number of replicates was caused by a shortage of newly emerged adults of this species.

A four-day period was allowed for oviposition. On the fifth day, the adults from each treatment were sieved off using a laboratory sieve of 2mm diameter apertures. They were then observed for mortality and placed with a fresh batch of grain to be removed after a further four days and so on.

This procedure was repeated over the full life span of both species to determine total fecundity and life span. Six to eight weeks after each sampling the adults that had emerged were counted and recorded. The task of counting the active weevils was done efficiently using a laboratory-made device working on vacuum.

3.3 Results

3.3.1 Oviposition pattern of each species

Oviposition of Sitophilus oryzae and S.granarius did not occur evenly throughout the life span. The pattern varied a great deal with grain species and with grain moisture content. Since temperature (25°C) and relative humidity (70%) were constant for all treatments, only the variables of grain species and grain moisture content could have been responsible for such differences in oviposition (and in fecundity and life span) of each species.

Figure 3.1 shows the number of eggs deposited (estimated from later emerged adults) by 100 newly-emerged S.oryzae and S.granarius in rice at 12% moisture content. The oviposition pattern for both species was closely similar in this treatment. Sitophilus oryzae reached its maximum egg laying soon after the start of the experiment, after which there were fluctuations (shown as 'peaks' and 'valleys' on the graph). Periods of increased oviposition usually lasted for about 12 days while periods of decreased egg laying lasted for only about four days.

Although similar, the pattern for S.granarius is slightly different in that the fluctuations occur at shorter intervals (about four days). Also in contrast to S.oryzae, S.granarius shows rather low oviposition at the beginning, after which it declines in a manner similar to that of S.oryzae.

Figure 3.2 shows results obtained with rice of 16% moisture content. The egg-laying pattern of S.oryzae in this case is at a much higher level than in rice of 12% moisture and shows very prominent 'peaks' and 'valleys'. The periods of increased oviposition also are longer than for 12% moisture content rice (lasting 12-21 days) and decrease sharply over a short time. These results indicate that conditions for oviposition in rice of 16% moisture content are more favourable for egg laying than in rice of 12% moisture content.

Sitophilus granarius oviposition in 16% rice is at a rate closer to that in rice of 12% moisture content. The main difference is that peak oviposition occurred about the 100th day, after which a gradual decrease took place. When compared with S.oryzae in this treatment, S.granarius has a lower overall oviposition rate. Periods of increase are short in contrast to the long periods for S.oryzae. This is clearly shown in the 3-point running mean curve (Figure 3.2.1).

In Figure 3.3, the oviposition rate of S.oryzae in 12% moisture content wheat shows fluctuations more pronounced than in 12% rice but decrease in the egg-laying rate begins about the same time as in 12% rice. Oviposition dropped very sharply to zero after 88 days.

The oviposition pattern of S.granarius in 12% wheat is one of less fluctuation without prominent peaks and valleys, as shown in Figure 3.3 and in the 3-point running mean curve (Figure 3.3.1). The oviposition rate decreased gradually without sharp drops and the total duration was short like that of S.oryzae.

The oviposition period for both species in wheat of 12% moisture content was thus less than that in rice in 12% and 16% moisture content.

As in rice, S.oryzae did better in wheat of 16% moisture content compared with 12% (Figure 3.4), and the overall egg-laying rate was very high as shown by the prominent and prolonged peak periods. However, the oviposition rate eventually dropped very sharply after about 70 days to low numbers.

S.granarius showed highest egg-laying rate in wheat of 16% moisture content compared with other treatments but after a period of high initial oviposition, there was a sudden drop to low numbers after about 30 days. This decrease occurred earlier than for S.oryzae under the same conditions. From then on oviposition fluctuated at a low level for some time before gradually decreasing to zero.

Overall, both species performed best in wheat of 16% moisture content.

In order to smooth out minor fluctuations in the oviposition graphs and confirm the existence of the peaks and valleys, the data was redrawn in each case in the form of a 3-point running mean curve. These are shown corresponding to the above figures and are numbered as Figures 3.1.1, 3.2.1, 3.3.1 and 3.4.1.

3.3.2 Fecundity

Total number of eggs laid by 50 females in each treatment has been tabulated in Table 3.1 (estimated from later emerged adults). Highest total was that for S.oryzae in 16% rice followed closely by the same species in 16% wheat. Rice of 12% moisture content was not favoured by S.oryzae for oviposition but in 12% wheat it performed somewhat better. The higher moisture content of 16% was clearly more favourable.

Sitophilus granarius followed a similar pattern to S.oryzae, but the total number of eggs laid was much less than for S.oryzae. In this case the least number of eggs was laid in 12% wheat and in 16% wheat while 16% rice was the most suitable. It also performed well in 12% rice.

From Table 3.1 it may be seen that S.oryzae showed the highest number of eggs per female in 16% wheat whereas S.granarius produced more similar numbers over all treatments.

The mean total progeny over all treatments (S.oryzae, S.granarius, rice, wheat, 12% moisture content, 16% moisture content) are presented in Table 3.2. S.oryzae produced the highest number of progeny (more than twice S.granarius). Rice was more favoured for oviposition by both insect species and 16% moisture content induced more eggs to be laid than 12%.

3.3.3 Longevity

The survival of adult S.oryzae and S.granarius in rice and wheat at 12% and 16% moisture content is shown in Figures 3.1.2, 3.2.2, 3.3.2, 3.4.2.

In rice of 12% moisture content, both S.oryzae and S.granarius showed 100% survival up to 52 days, after which mortality progressively occurred, but at a lower rate for S.granarius than for S.oryzae. The latter showed a sharp increase in mortality after 116 days, and at 156 days there were less than 10% still surviving.

Fifty percent mortality of adult S.oryzae was reached after 120 days and of S.granarius after 152 days. Mean life span for S.oryzae in this treatment thus was shorter than that for S.granarius.

In rice of 16% moisture content, S.oryzae showed very low mortality (Figure 3.2.2), which was less than 50% at the end of the experiment (156 days). In contrast to 12% rice, S.oryzae survived better in 16% rice than S.granarius.

S.granarius lived longer in 16% rice than in 12% rice and displayed a steady mortality rate. It reached

50% mortality after 148 days. Richards (1947) found that at 25^{o}C and 70% R.H. mass cultures of this species similarly showed 50% mortality after 22 weeks (154 days).

Survival rate in 12% wheat was similar for both Sitophilus species, with S.oryzae surviving slightly better. S.oryzae showed 50% mortality after 92 days, slightly earlier than in 12% and 16% rice. S.granarius was very similar, attaining 50% mortality after 100 days.

Figure 3.4.2 shows survivalship curves for both species in 16% wheat. S.oryzae reached 50% mortality after 88 days whereas S.granarius showed a sharp decrease in survival at the very beginning and reached 50% mortality after 44 days, after which numbers declined only gradually.

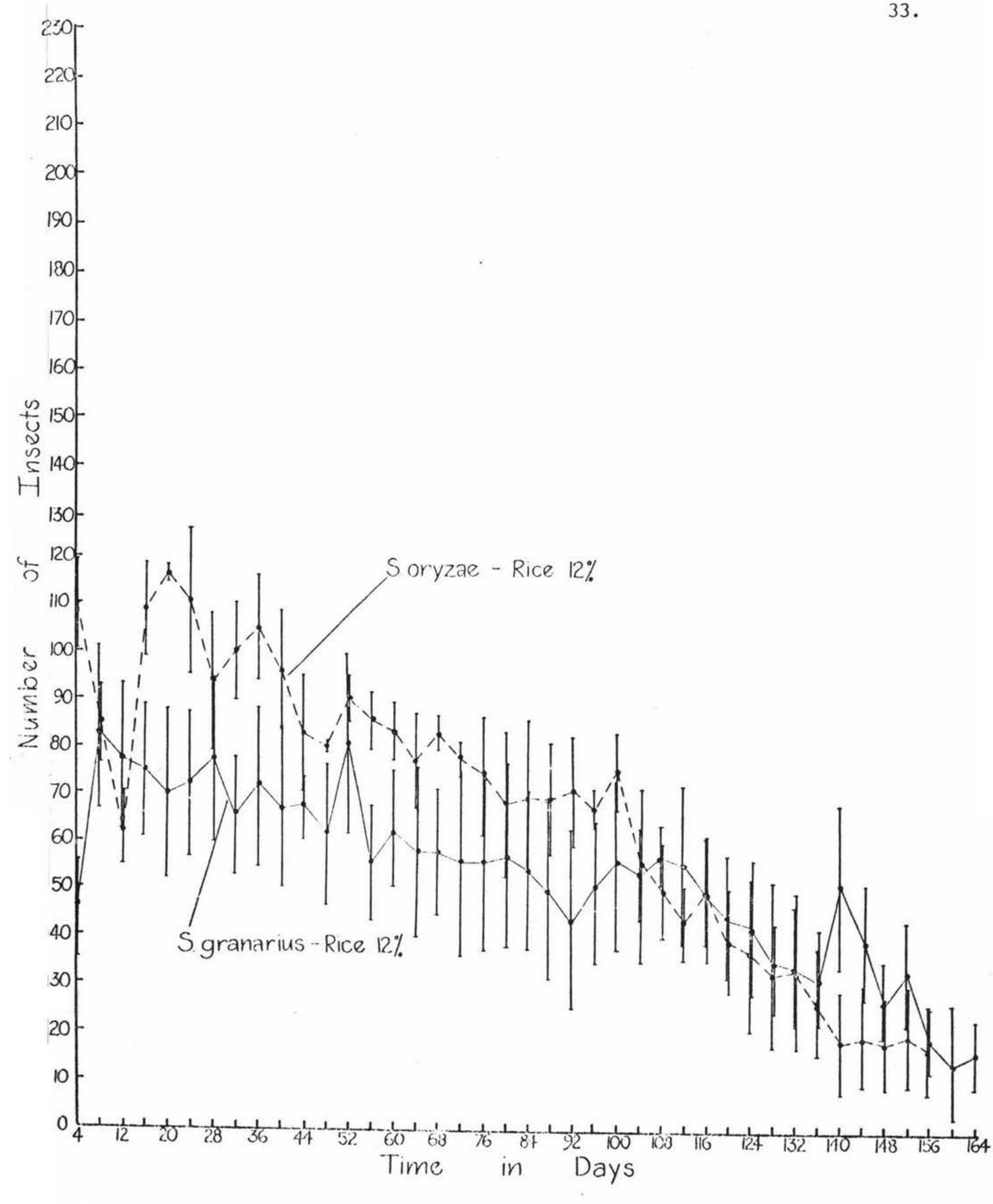


Figure 3.1: Mean oviposition rate of S.oryzae and S.granarius in rice 12% moisture content. Vertical bars represent S.E. of the mean.

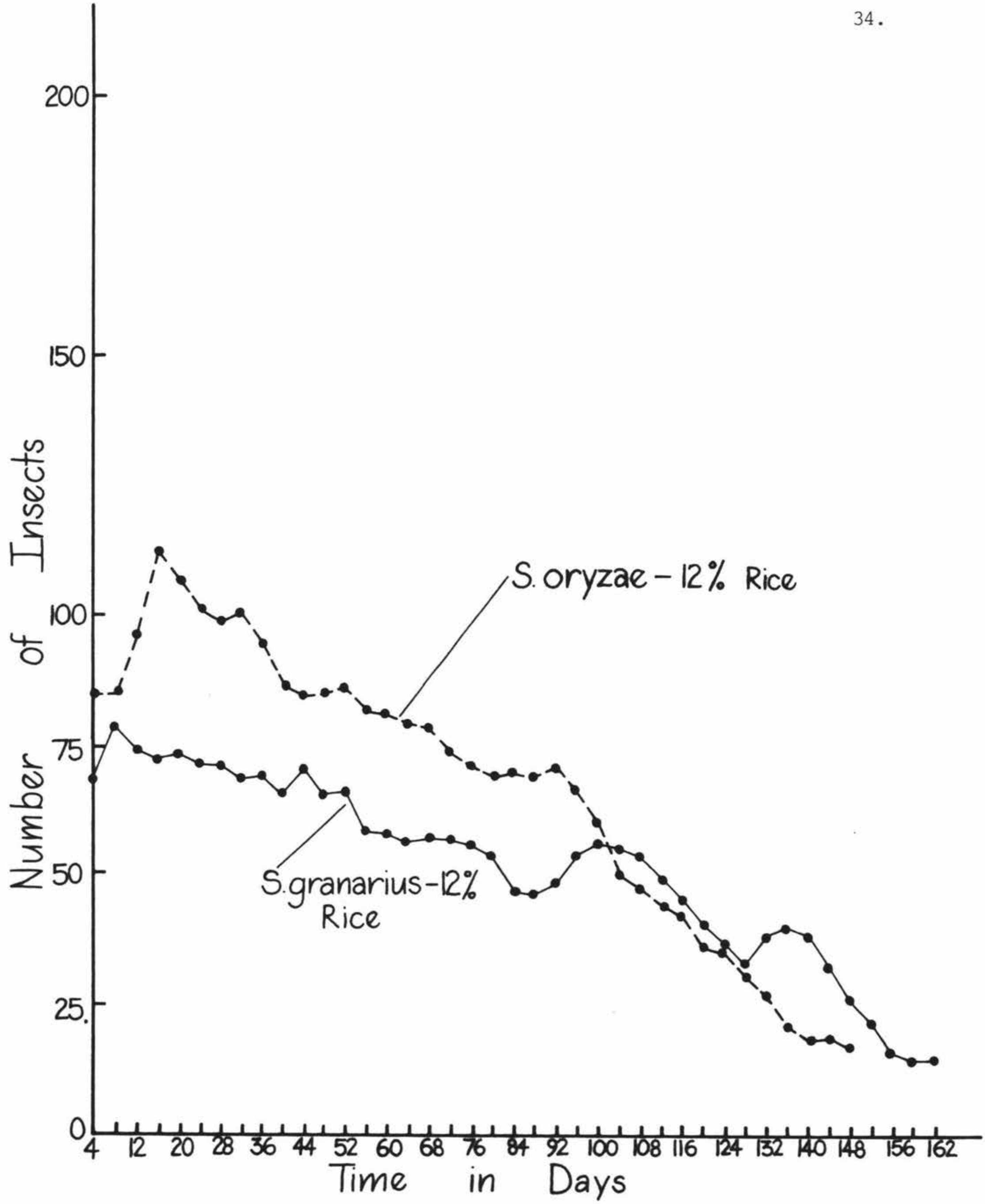


Figure 3.1.1: Three-point running mean of oviposition rate of S.oryzae and S.granarius in 12 percent rice

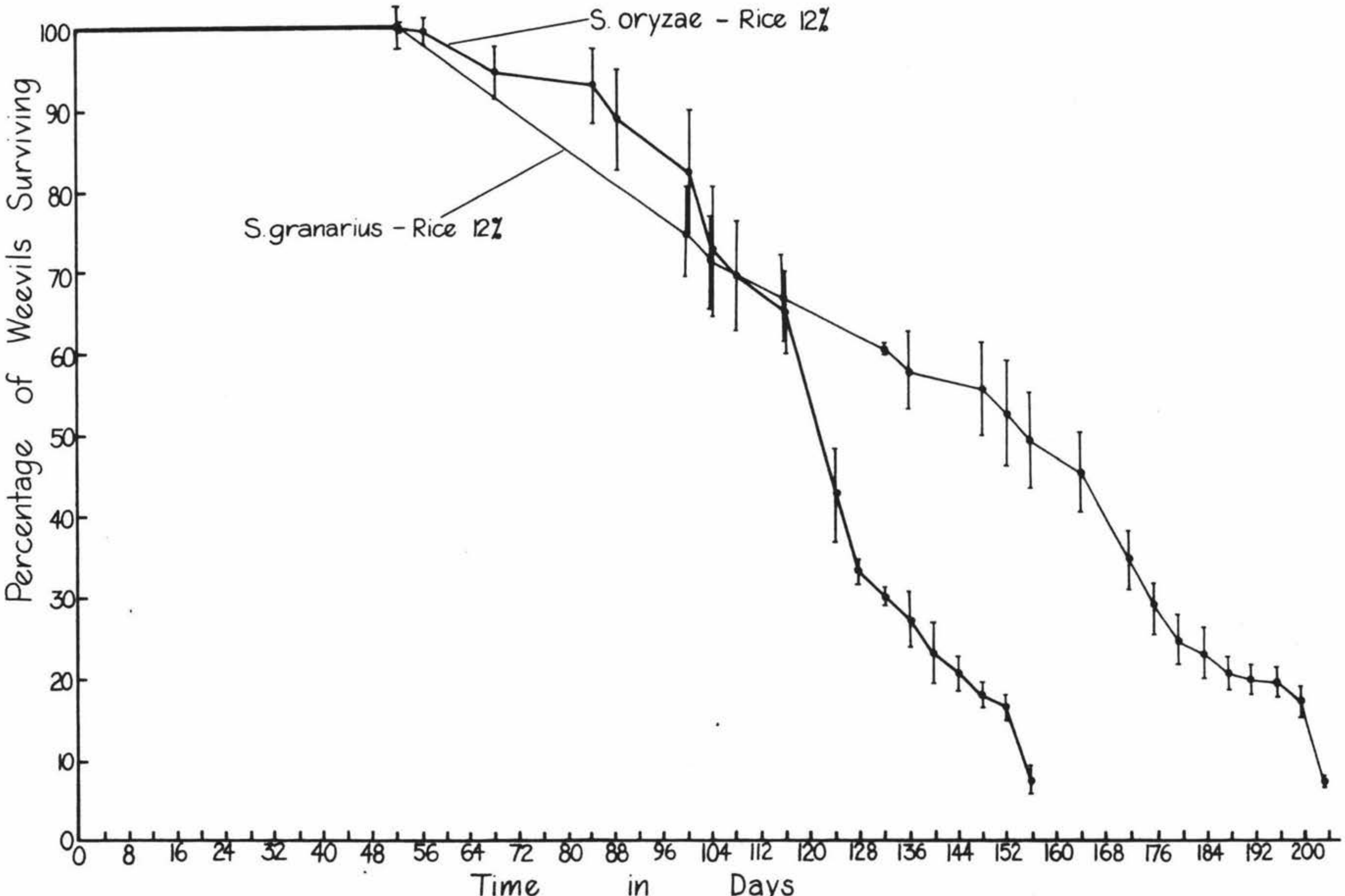


Figure 3.1.2: Mean survivalship curves of 100 adult S.oryzae and S.granarius in 12% rice. Vertical bars represent S.E. of the mean.

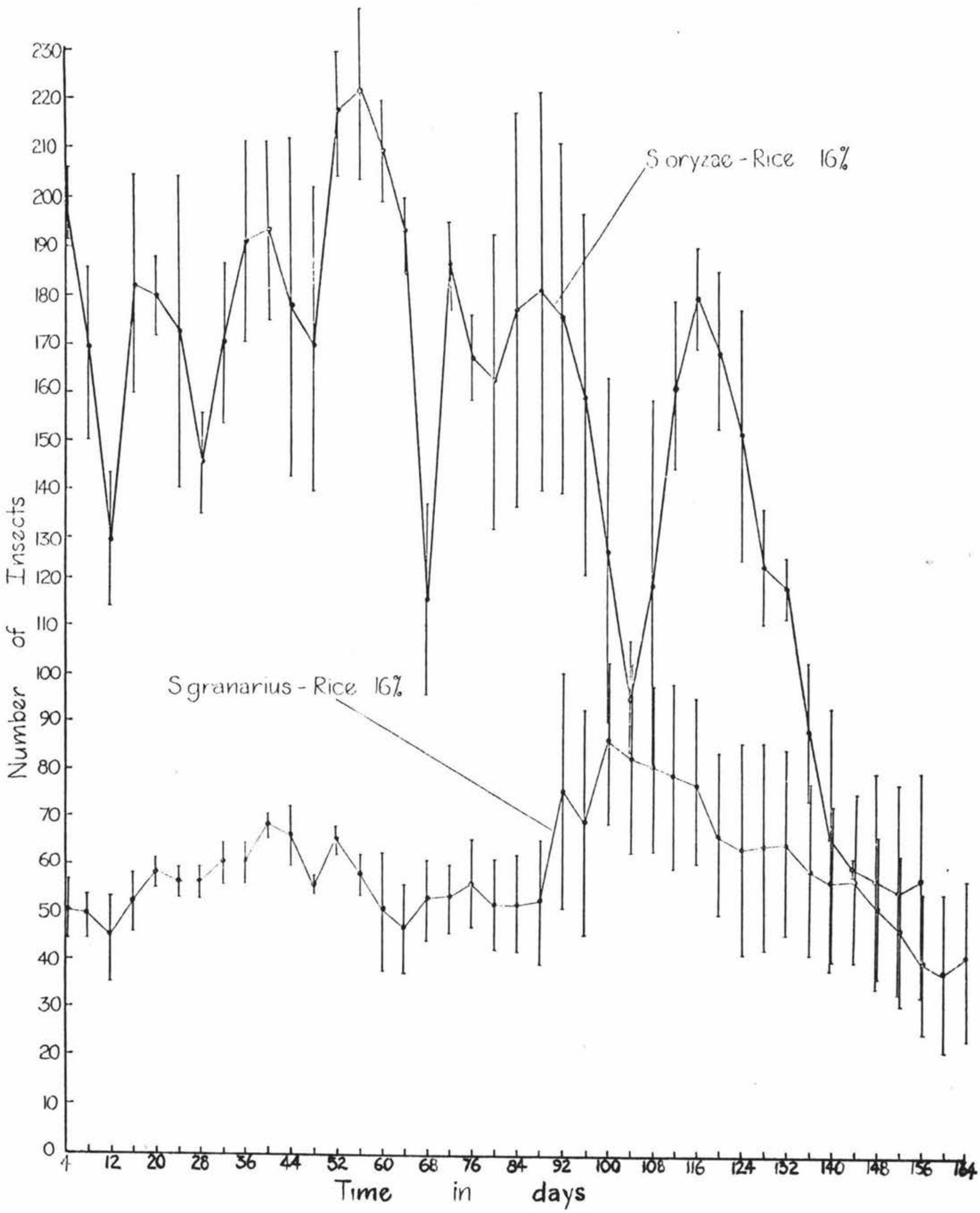


Figure 3.2: Mean oviposition rate of S.oryzae and S.granarius in 16% rice. Vertical bars represent S.E. of the mean.

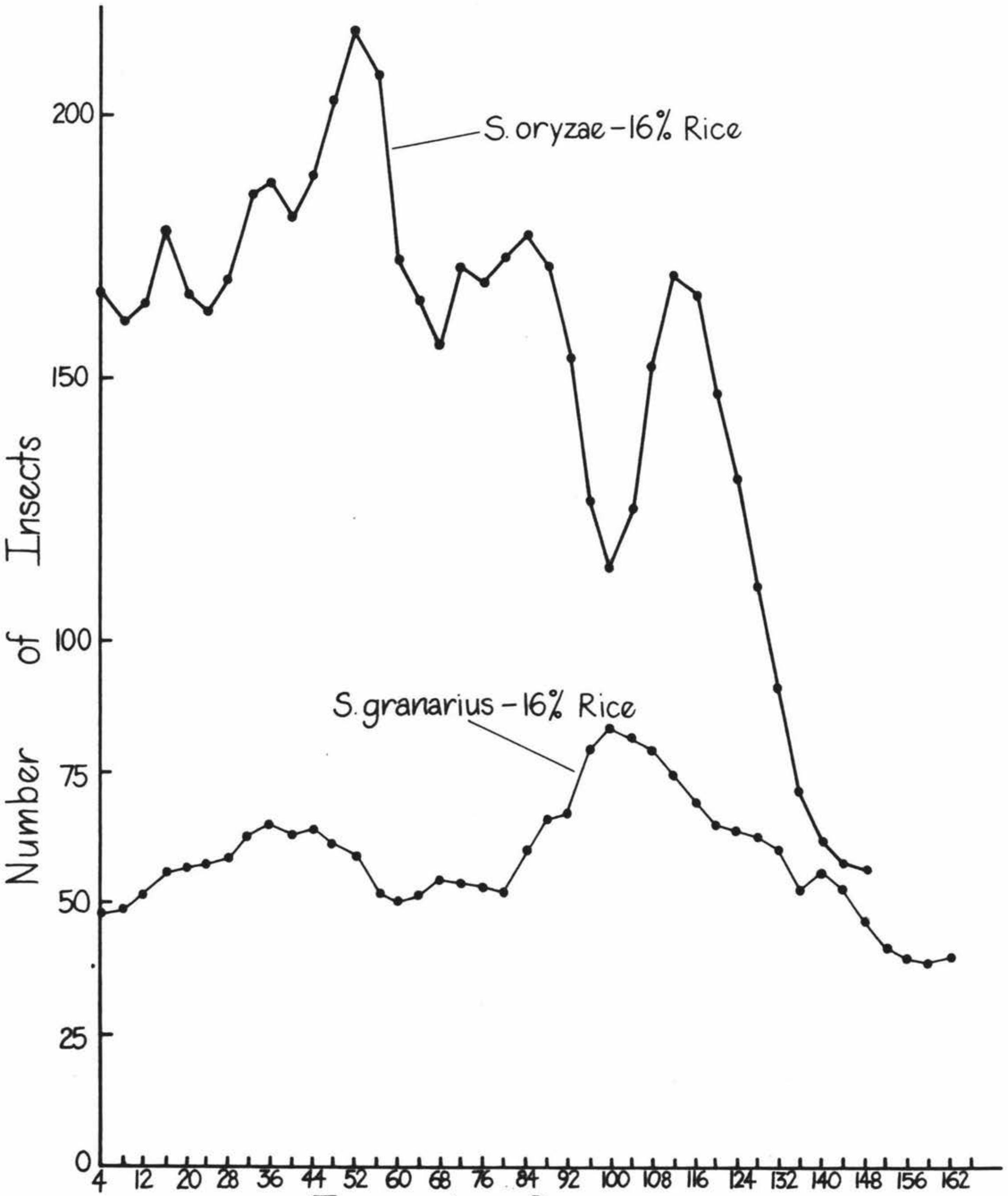


Figure 3.2.1: Three-point running mean of oviposition rate of S.oryzae and S.granarius in 16% rice

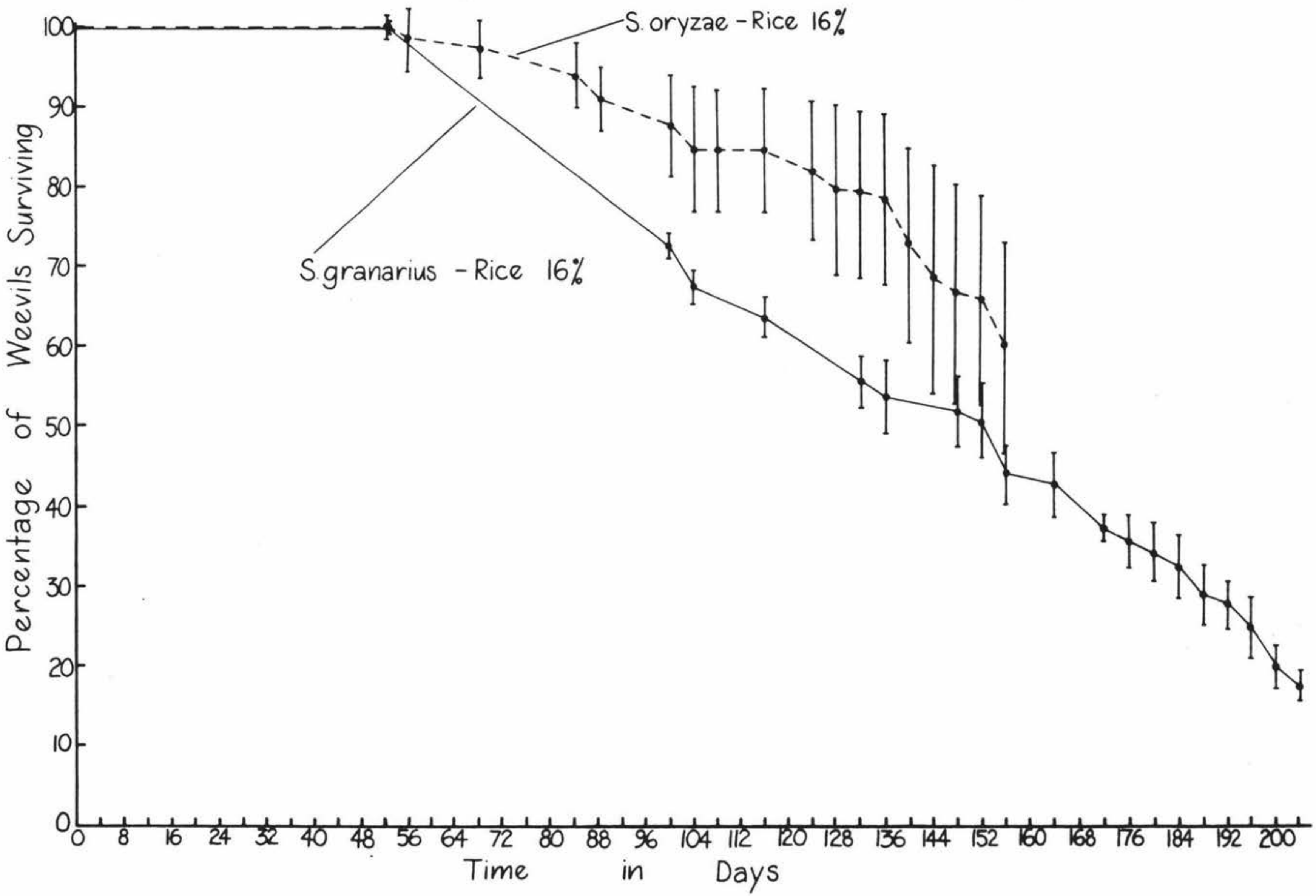


Figure 3.2.2: Mean survivalship curves for 100 adult S.oryzae and S.granarius in 16% rice. Vertical bars represent S.E. of the mean.

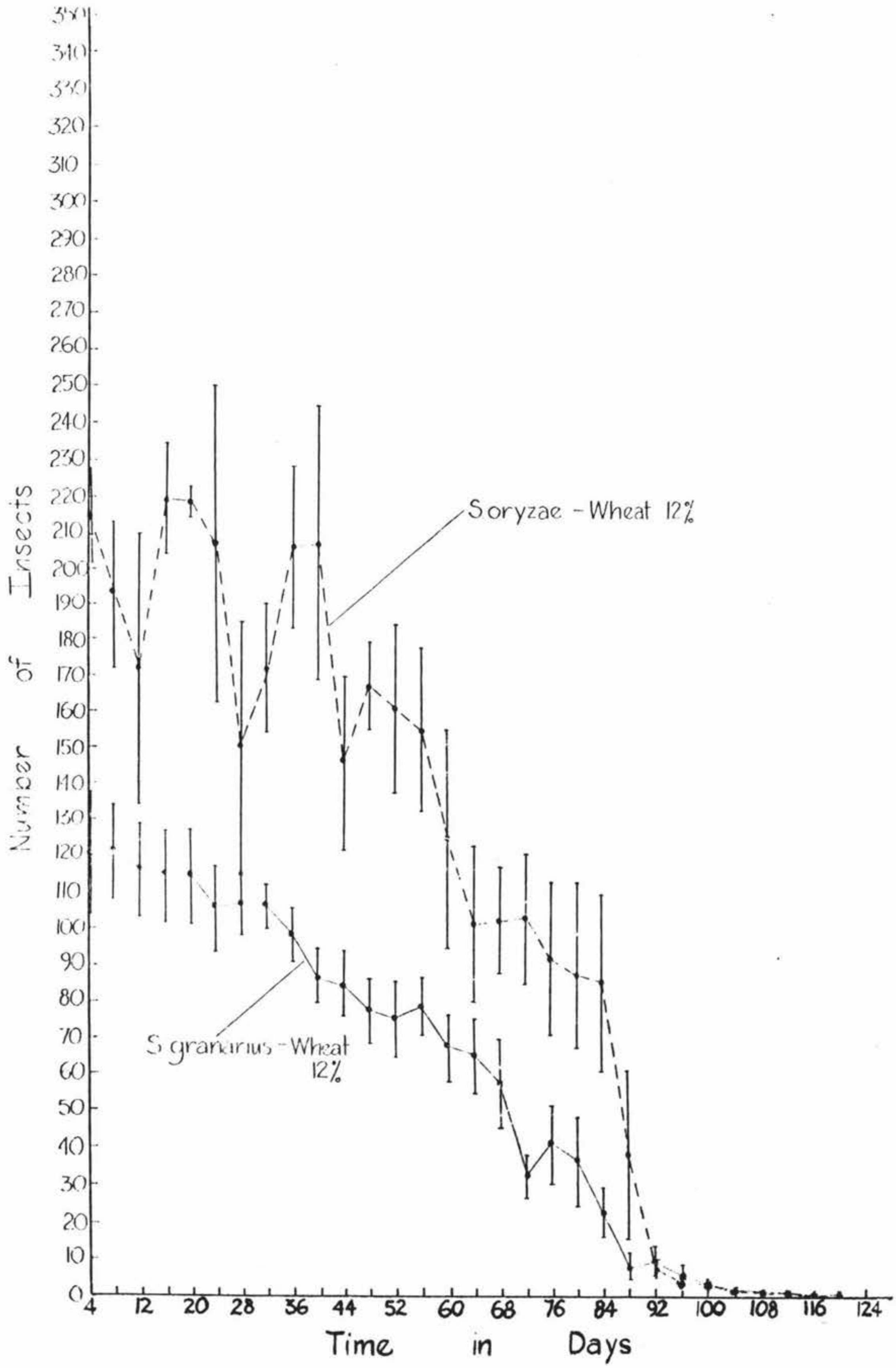


Figure 3.3: Mean oviposition rate of S.oryzae and S.granarius in 12% wheat. Vertical bars represent S.E. of the mean.

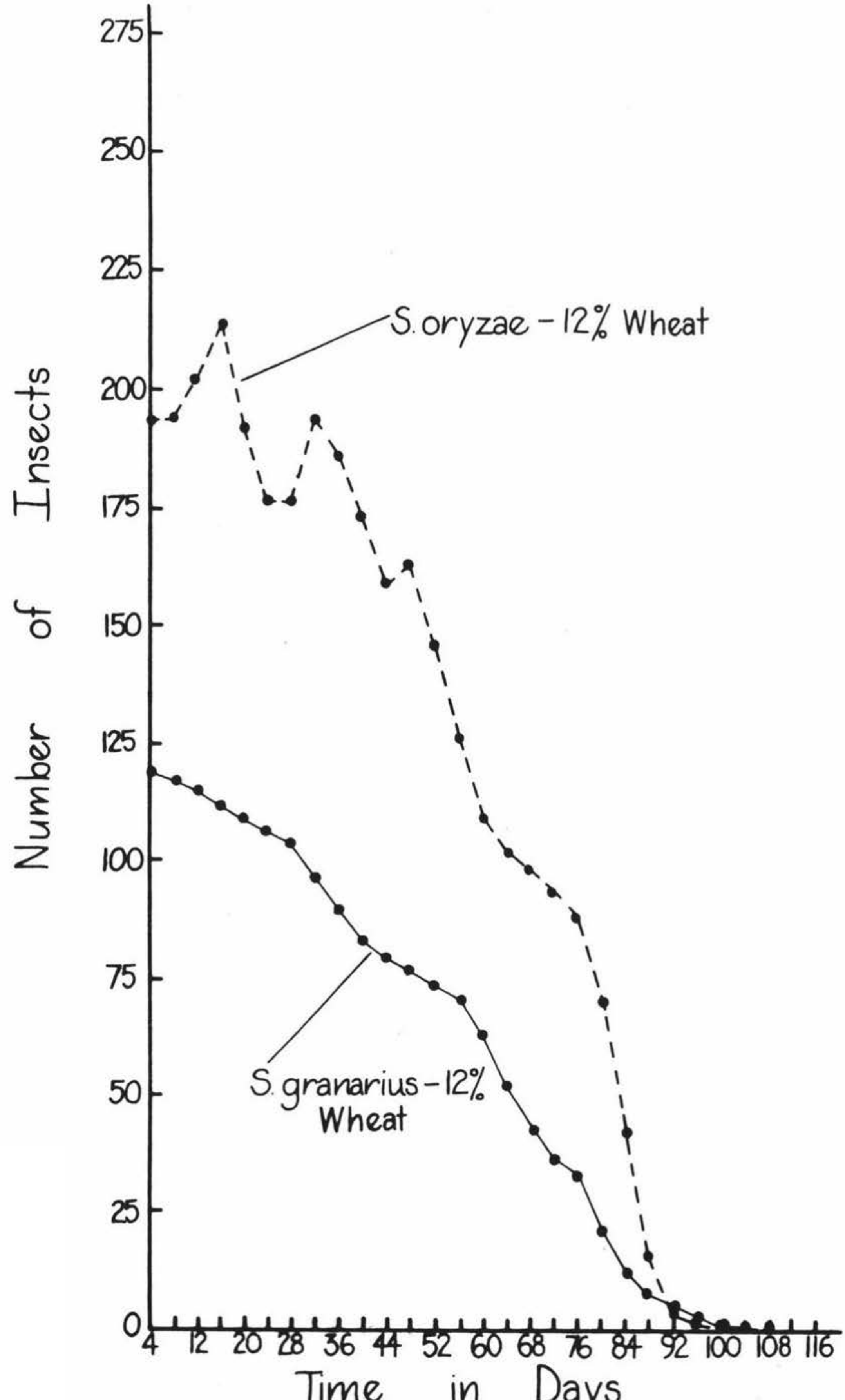


Figure 3.3.1: Three-point running mean of oviposition rate of S.oryzae and S.granarius in 12% wheat

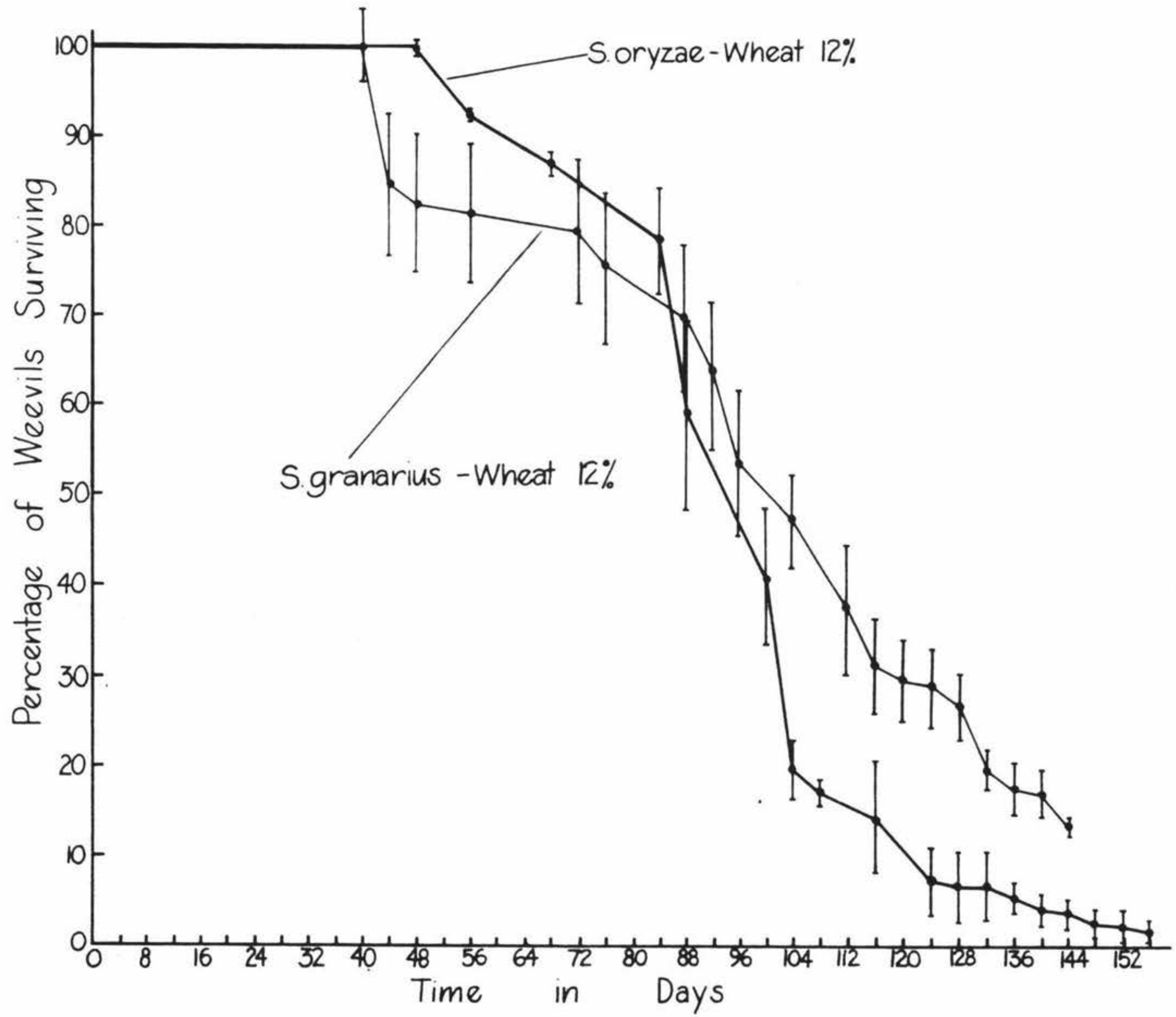


Figure 3.3.2: Mean survivalship curves for 100 adults of S.oryzae and S.granarius in 12% wheat. Vertical bars represent S.E. of the mean.

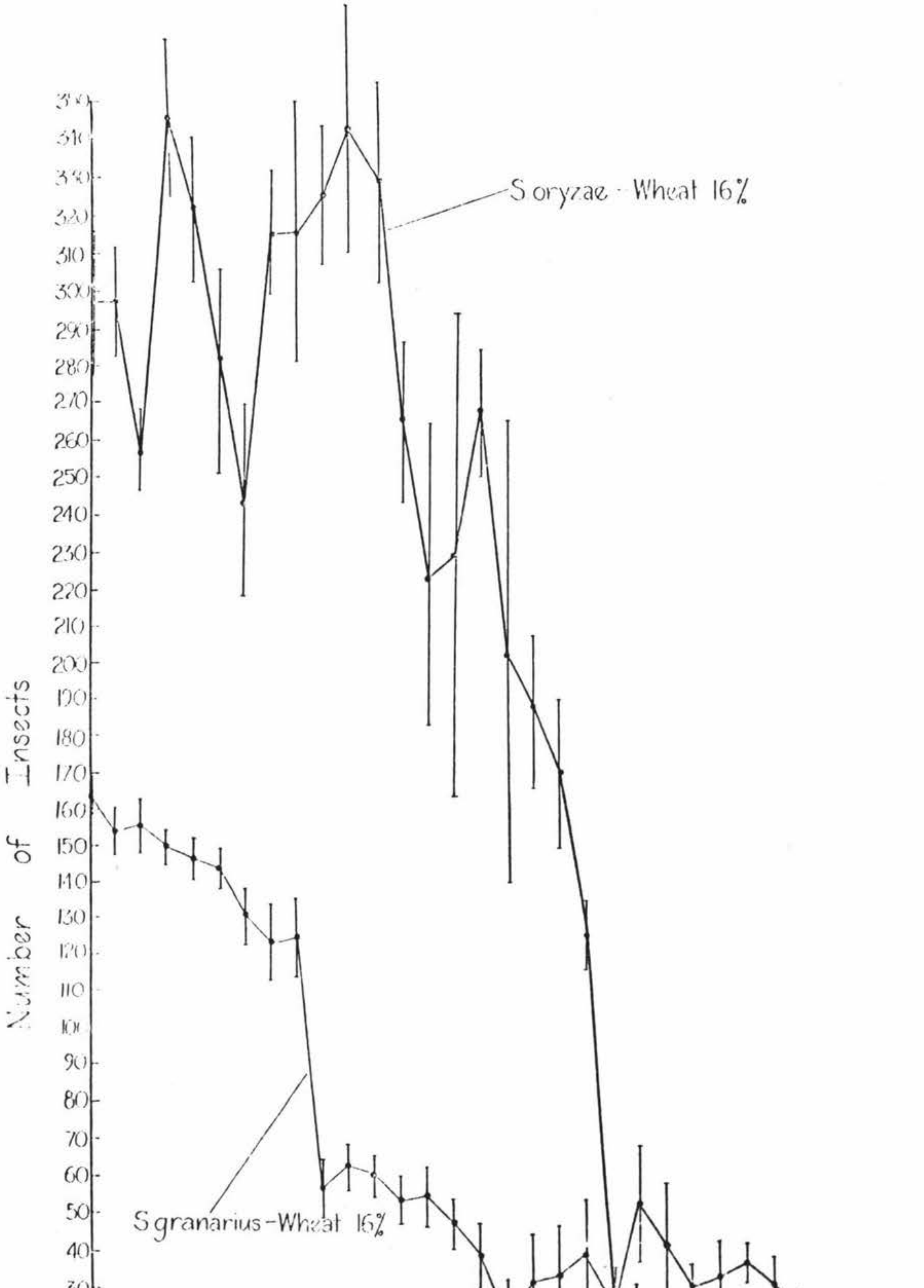


Figure 3.4: Mean oviposition rate of S.oryzae and S.granarius in 16% wheat. Vertical bars represent S.E. of the mean.

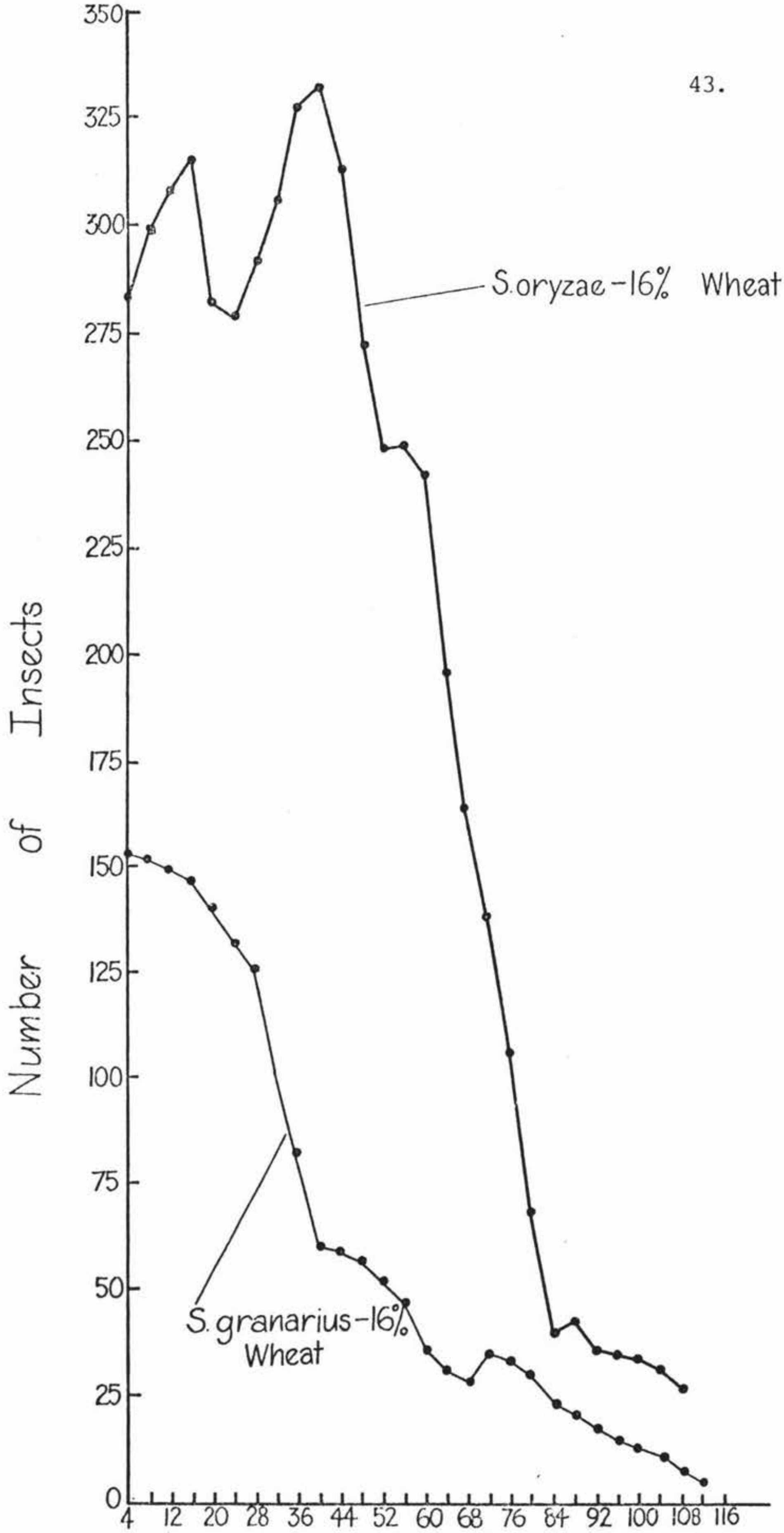


Figure 3.4.1: Three-point running mean of oviposition rate of S.oryzae and S.granarius in 16% wheat

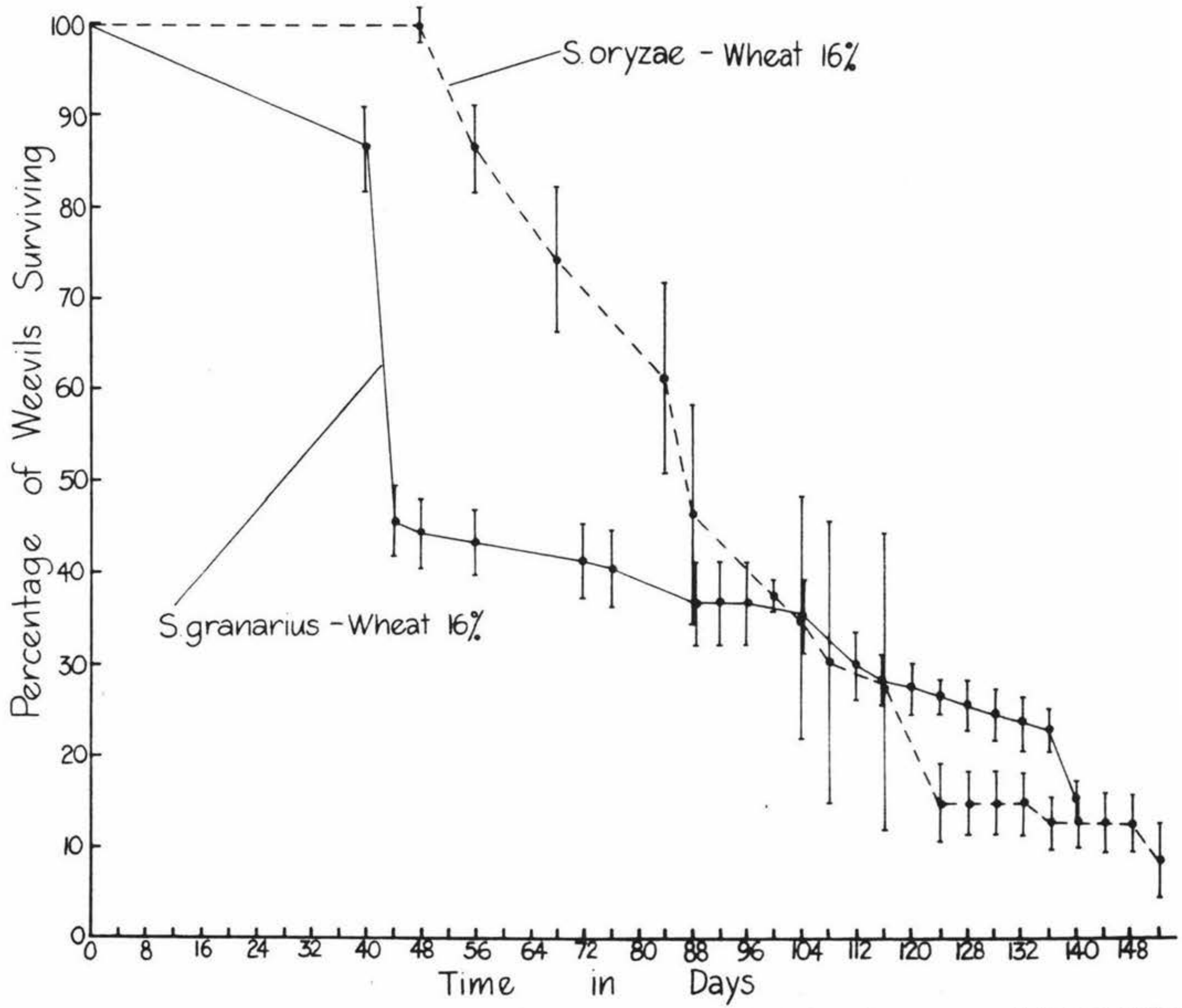


Figure 3.4.2: Mean survivalship curves for 100 adults S.oryzae and S.granarius in 16% wheat. Vertical bars represent S.E. of the mean.

Table 3.1: Total numbers of adult progeny during the reproductive life of one hundred adult Sitophilus oryzae and S.granarius in 12% and 16% grain moisture content rice and 12% and 16% wheat

Treatments under 25°C 70% R.H.	Mean total progeny per 50 females	Mean life span in days	Mean progeny per female (I.S.E.)
Sitophilus oryzae			
12% Rice	2614	156	67 (± 20.9)
16% Rice	5881	156 *	150.8 (± 33.1)
12% Wheat	3344	116	115.3 (± 56)
16% Wheat	5612	116	193.5 (± 86.6)
Sitophilus granarius			
12% Rice	2196	172	51.1 (± 10.9)
16% Rice	2520	172	58.6 (± 7.1)
12% Wheat	1756	120	58.5 (± 26)
16% Wheat	1928	120	64.3 (± 31.6)

* More than 50% of the initial 100 were still alive at the conclusion of the experiment

Table 3.2: Mean total progeny for Sitophilus oryzae and S.granarius in rice and wheat grain with moisture contents of 12 and 16 percent ($25^{o}C$ and 70% R.H.)

	Insect Species		Grain Species		Grain Moisture Content	
	S. Oryzae	S.Granarius	Rice	Wheat	12%	16%
Mean Total Progeny	4363	2101	3303	3160	2043	3508

3.4 Discussion

Considerable data are available concerning rates of development of Sitophilus species but little for the pattern of oviposition. Howe (1965) stressed the point that beetles have a long adult life and therefore, the pattern of oviposition has a strong influence on their rate of increase.

In this experiment oviposition generally reached a peak in the second or third week, then fluctuated for a while before declining. This pattern was seen in different degrees in each treatment as seen in the results section (3.3). In the treatments using rice of 12% and 16% moisture content, both Sitophilus species performed better in the higher moisture content but the difference was much less for S.granarius than for S.oryzae. In those treatments using wheat, both species again had highest egg-laying rate at 16% rather than 12% with the difference also most marked for S.oryzae. Between the two types of grain there was overall a slightly higher oviposition in rice than in wheat but the difference was much more marked for S.oryzae than for S.granarius. These results show that an increase in grain moisture content from 12% to 16% increases the rate of oviposition markedly in S.oryzae, but has little effect on S.granarius.

Since the oviposition patterns in the present study involve estimated egg numbers from later emerged numbers, this may underestimate the number of eggs laid as there may be mortality occurring from egg to adult stage. Birch (1944b), however, showed that at 25°C and 70% R.H. mortality of S.oryzae from eggs to adult was low and Longstaff (1981) summarised work done by MacLagan and Dunn (1935), Birch (1944b, 1945b), Howe (1952), Howe and Hole (1968), Hardman (1978) and Kirkpatrick (1978) which showed that mortality of the immature phase is lowest in the temperature range of 20-30°C and at relative humidities above 60%. Howe (1952) found that only 10% mortality of egg and larval stages occurs at optimum conditions. Errors in estimating oviposition rate from numbers of later emerged adults are probably therefore small.

Birch (1945) working with wheat at 14% moisture content showed that at 25^{O}C, oviposition reached a peak in the second or third week and subsequently declined. In the present study, the minimum egg-laying period was from the second or third week, fluctuating from then on in various degrees according to treatment. Birch, however, found that the rate of oviposition after the second or third week was 'fairly steady' for 10-12 weeks in contrast to the present results. Birch also showed that oviposition is little affected by grain moisture content above about 14%, although it was markedly reduced at 12% and below. According to the present study this only applied to S.oryzae as very little variation in the oviposition pattern of S.granarius was seen.

In the present study it was also noticed that S.oryzae begins to oviposit earlier than S.granarius at 25^{O}C. This has been previously shown by Steffan (1963) and Howe and Hole (1967) who stated that S.granarius only began ovipositing after 5-6 days.

Oviposition of Sitophilus oryzae and of S.granarius was highest and most constant between 10-36 days in wheat of 12 and 16% moisture content. This agrees well with the results of Howe and Hole (1967) who found that oviposition was greatest from 10-30 days. Birch (1945), however, obtained maximum egg-laying between 70 and 84 days.

The maximum egg-laying period in rice lasted longer than in wheat for both Sitophilus species, the high oviposition rate lasting only a short while in wheat of both 12 and 16% moisture content. Cotton et al (1960) suggested that up to a certain point an increase in the moisture content of grain causes a corresponding increase in the rate of reproduction but that moisture contents above 15% although at first favourable, later result in the population dying out. The later decline in oviposition rates in all treatments could be due simply to aging of the weevils as Howe and Hole (1967) claimed that oviposition rates declined as the adults aged. While this is doubtless partly true in this study, type of grain (rice or wheat) and moisture content of grain appear to have a greater influence.

The mean fecundity for S.granarius in the present study (Table 3.1) is much less than that reported by Surtees (1964) (220 offspring per female) and Howe (1967) (185 offspring per female). The lower fecundity in the present study could be due to the limited availability of grain for oviposition. Howe and Hole (1966) assumed that 1.5 beetles per gramme of grain gave satisfactory cultures, and Howe (1967) used 100 adults to 100g of wheat. These ratios are a lot higher than in the present study. This factor, therefore, may have caused overcrowding and less eggs laid as a result of fewer grains per female. Birch (1945) gives a very high fecundity for S.oryzae of 720, although this value had been corrected for larval mortality by Longstaff (1981). Birch (1945c, d) used one female to 500 grains whereas in the present study only 4 grains were allotted per adult. These differences could well explain the lower fecundity obtained in this study.

Fourie (1967) found that when exposed to different treatments (10 and 14% moisture content and 22^{o}C and 26^{o}C temperatures), maximum fecundity of S.oryzae occurred at 26^{o}C and 14% moisture content of maize. In the present study this agreed with the results for S.oryzae but S.granarius did not show marked variation. As for rate of oviposition as seen earlier, S.granarius does not seem to be much affected by different moisture contents. Ungsunantwiwat and Mills (1979) reported that S.oryzae laid an average of about 183 eggs in wheat at 13-14% moisture content and S.granarius laid an average of about 65 eggs. These results tallied with that of the present study.

According to Ewer (1945) grain size is important for successful oviposition by S.granarius. Therefore, the lower fecundity in S.granarius observed in this study may be due to the unsuitability of the physical nature of grains provided.

A further possible cause of discrepancy from other published data is that the particular strain of S.granarius used in the present study could be altogether low in productivity as Satomi (1960) found considerable variation in the oviposition rate of several strains of S.zeamais and S.oryzae. Kiritani (1965) and Soderstrom and Wilbur (1966) also found considerable differences within the same two species. Working with S.granarius under various temperatures and humidities, Eastham and McCully (1943) showed that as long as a female has access to food, the same number of eggs are laid at 20°C or 27°C but that the rate of egg laying may differ.

In studying the effect of food on oviposition of S.oryzae, Floyd and Newsom (1959) and Kono (1960, unpublished) reported that the greatest number of progeny was produced on rice and that wheat was second. In the present study, rice also was favoured to wheat by both Sitophilus species (Table 3.2). Ungsunantwiwat and Mills (1979) found that reproduction in wheat, sorghums and maize was highest when parents had been earlier reared in wheat. In the present study weevil colonies had been maintained on wheat.

In all the treatments, adult survival of S.oryzae was nearly 100% up to 50 days except in rice of 16% moisture content where more than 50% were still alive at the end of the experiment (156 days).

A similar pattern was seen for S.granarius in all treatments except for 16% rice where mortality began from the start. Overall, S.granarius was longer lived than S.oryzae (Table 3.1) which agrees with the data of Richards (1947) who found a mean life span of 175 days for S.granarius. Longstaff (1981, unpublished) reported a similar life span for S.oryzae.

In all cases, the mortality during the peak reproductive period was low but it increased with age (Birch, 1953a). Howe and Hole (1967) observed a similar trend. Coombs and Woodroffe (1963c) reported that longevity of S.granarius on wheat was slightly less than Richards (1947) recorded. MacFarlane (1968) stated that greater longevity may arise from a low oviposition rate on rice. This appears likely as S.granarius, which lived for a longer period than S.oryzae, gave rise to fewer progeny (Table 3.1).

Both S.oryzae and S.granarius suffered greater mortality at lower grain moisture content as found by Robinson (1926). The rapid death of the population of S.granarius in 16% wheat (50% mortality in 44 days) was unexpected as high grain moisture content is not normally associated with high early mortality. Similar mortality occurred when Coombs and Woodroffe (1963c) were studying the influence of food condition on the longevity of Sitophilus granarius but this was in a long term experiment and after about two years. Their explanation was that the food materials (grain and flour) might have become contaminated by the dense weevil population so as to render them toxic. They suggested that such toxicity might be highly species specific.

In the present study where fresh food was provided every four days, such an explanation cannot apply. Also, the same grain (wheat 16%) was used for treatments with S.oryzae and similar marked mortality did not occur. Coombs and Woodroffe (1963c) have suggested that it may be advisable to use husk or frass in experimental grain media to prolong the life span of adult S.granarius.

The environmental factors employed in this experiment - temperature, relative humidity, types of grain and grain moisture content - may have acted in several ways. For example, food may provide fully or incompletely the materials necessary to sustain life and produce eggs (Mellanby, 1934a). It is the integration of these factors in the life of the weevils which determine their behaviour, setting a limit to the length of life, rate of oviposition and therefore, to the total number of eggs produced during a life-time (Eastham and McCully, 1943). As temperature and relative humidity were constant, and both close to optimum, for both Sitophilus species differences between treatments can only be a function of grain species or seed moisture content.

Grain is hygroscopic and tends to reach an equilibrium moisture content depending on the atmospheric relative humidity of the storage conditions. This however, may take several weeks, and as the grain of different moisture contents (12% and 16%) was replaced every four days in the current experiment, moisture content is unlikely to have changed significantly during the course of an experiment even though all samples were stored at one humidity level of 70%. This does not apply to the longer term experiments concerned with population growth described in Chapter Five.

Eastham and McCully (1943) state that any condition of food which renders it less acceptable and less easily masticated and digested must serve as a deterrent to egg production. They also claim, therefore, that length of life, rate of oviposition and number of eggs laid in part, depend on grain moisture content. Eastham and McCully also stated that as most researchers had worked with starved insects, death in many cases was due to starvation following the exhaustion of food reserves or inability to use those reserves as other conditions of life became severe.

CHAPTER FOUR: RATE OF DEVELOPMENT OF LIFE STAGES OF SITOPHILUS ORYZAE AND S.GRANARIUS

4.1 Introduction

The developmental stages of the rice weevil Sitophilus oryzae L., and granary weevil S.granarius L. are passed inside the kernels of stored cereals and for this reason it is easy to handle them safely in large numbers as Howe and Hole (1967) realised. The two species have similar life cycles. The female deposits an egg inside an excavated hole in the grain and seals the hole with a gelatinous plug. Frankenfeldt (1948) and Sharifi (1972) give details of how to detect such plugs.

Eggs are usually laid farthest from the embryo in cereal grains (Richards, 1947). Sometimes, more than one egg may be laid in a single grain, and although it is rare for more than one larva to develop to an adult due to cannibalism, this does sometimes occur.

There are four larval instars all of which remain within the grain. Soon after hatching, the first instar larva feeds vigorously by burrowing through the grain. Towards the end of the fourth instar the larva uses a mixture of frass and larval secretion to close off the end of the burrow to form a pupal cell. For about one day the larva is in a whitish prepupal form before becoming a pupa. When the adult has developed, it remains within the grain for several days before emerging. The extent of this period varies with temperature.

Although several authors have investigated the duration of the developmental stages of Sitophilus, only the data of Khan (1947), Soderstrom (1960) and Ungsunantwiwat and Mills (1979) permit direct comparisons to be drawn between the species S.oryzae and S.granarius.

Although early work on duration of development was done by Cole (1906) on S.oryzae and Anderson (1934) on S.granarius, Longstaff (1981) in his review of the biology of the genus Sitophilus concludes that the study by Eastham and Segrove (1947) is the most comprehensive to date. They determined the duration of the developmental period of S.granarius over a range of temperature and humidity conditions and found that in general the development period shortens as temperature and/or humidity increases. The effect of grain moisture level on the duration of the individual stages varies, with eggs and pupae being largely unaffected whilst all larval stages show marked responses. S.oryzae shows basically similar patterns of response to different temperature and moisture conditions. Reddy (1950a, b) and Hardman (1978) both found that the developmental period was protracted at temperatures above 30^{o}C. Geographic variation in the duration of the immature phase has been found in some instances (Satomi, 1960).

Howe (1967) considered the effect of parental age on the duration of the developmental period and found that there was a parabolic relationship with the longest period occurring with parents of middle age. Golebiowska (1969) and Evans (1977a) found that maternal age appeared to have only a slight effect on the duration of the developmental period. (With increasing maternal age, the developmental period increased). In the present study, this factor was not investigated.

An attempt was made in this study to extend the information of Chapter Three (rate of egg-laying, number of eggs laid and the life span of S.oryzae and S.granarius) by showing how environment determines the total duration of the developmental period.

4.2 Materials and methods

4.2.1 The experimental design

The grain used for this experiment was prepared in the same way as the preliminary experiment already discussed. A stereo microscope was used to enable observations to be made of eggs and early larval instars. Five hundred mixed aged adults of *Sitophilus granarius* were placed with 500 grains of unpolished rice or whole wheat at 12% moisture content. The same number was placed with 500 grains of unpolished rice or whole wheat at 16% moisture content. These treatments had no replications.

Similar treatments were set up using 500 mixed aged adults of *Sitophilus oryzae*.

Half litre glass jars with screw top rings fitted with wire gauze were used.

4.2.2 Oviposition period

A 48 hour period was allowed for oviposition then the adults from each jar were sieved off. Twenty five grains from each treatment were removed every alternate day, soaked in alcohol and dissected under the microscope for eggs and larval instars.

4.2.3 The egg

The egg was seen as a rounded, transparent soft outer membrane enclosing an opaque mass. The eggs of *Sitophilus granarius* and *Sitophilus oryzae* were indistinguishable. In order to determine the duration of the egg stage, the grains were dissected every day until the first larval instars were observed. This was taken to be the hatching or incubation period (Khan, 1949).

4.2.4 The larval instars

There were four larval instars, the last being the prepupal stage. The grains were checked daily to ensure that instar changes were carefully observed.

4.2.5 The pupa

The duration of the pupal stage was determined similarly until emergence of the adult.

4.2.6 The adult weevil

The adults emerged over lengthy periods since they remain inside the grains for 2-3 days and sometimes even longer at high temperatures and humidities. At low temperature, the adults may stay for weeks (Khan, 1949) inside the grain.

4.3 Results

The data obtained for Sitophilus oryzae are presented in Figures 4.1, 4.2, 4.3 and 4.4 and for S.granarius in Figures 4.1.1, 4.2.1, 4.3.1 and 4.4.1. Each figure shows the duration of each developmental stage from egg to adult emergence and the range of time in each stage. The head capsule width at each larval instar is also presented.

These results vary very little from those published by other workers. Table 4.4.1 in the discussion section (4.4) summarises the duration of the developmental stages in S.oryzae and S.granarius according to data obtained by different workers for similar conditions used in this study.

There were some apparent differences in the present study between the two grain species and between the two seed moisture contents (12% and 16%). Overall, both S.oryzae and S.granarius took longer to develop in 12% than in 16% IMC seed (Figure 4). However, when comparing the duration of development between S.oryzae and S.granarius, S.oryzae took a shorter time to complete development than S.granarius in wheat and in rice of 12% IMC, while the opposite occurred in rice of 16% IMC. The significance of such differences are shown in Table 4.1.

Head capsule widths of the four larval stages of both Sitophilus species are shown in Figs. 4.1 - 4.4. Head capsule widths of all four larval instars of S.oryzae were less than for S.granarius. The data from the present study corresponded with that of Richards (1947).
(IMC = Initial Moisture Content)

4.3.1 Duration of egg stage

The mean duration of the egg stage is given in each figure (4.1 - 4.4 inclusive) for each Sitophilus species. The mean egg period is more or less similar in all treatments. Longstaff (1981) presented a table with mean duration for each stage (egg to adult) as determined by various workers. The present data agree with these published values.

4.3.2 Duration of larval stages

The range of developmental time for each instar is shown by the sloping solid line with respect to the vertical broken line in each graph (Figures 4.1 - 4.4). Mean width of the head capsule for each instar is marked as a dot on the graph.

4.3.3 Duration of pupal stage

The duration of the pupal stage is shown for each treatment (Figures 4.1 - 4.4 inclusive).

4.3.4 Adult stage

There was often a delay in emergence of the weevil from the grain after the insect had freed itself from the pupa. It should therefore be understood that 'adult emergence' means emergence from the pupa and not from the grain. This usually took about 5-6.5 days. The data of Richards (1947) and Sharifi and Mills (1971b) were similar to the present study.

Table 4.1 shows the total developmental period from egg to adult stage in each grain species at each moisture level (12 and 16%). There was a significant difference (in the total developmental period) between the Sitophilus species in 12% wheat with S.granarius having a significantly longer developmental period. However, in 16% wheat there was no significant difference between the species. The only other significant difference between developmental times was for S.granarius between wheat of 12 and 16% moisture content.

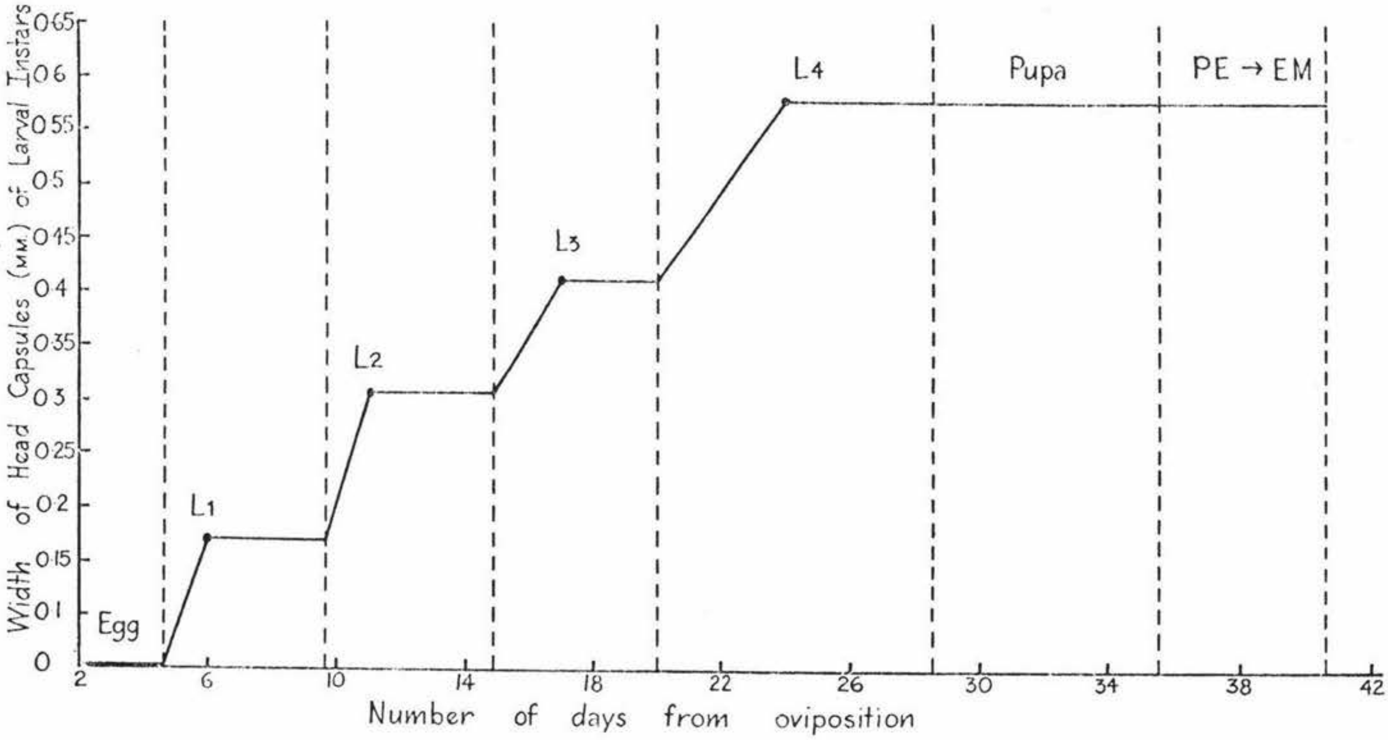
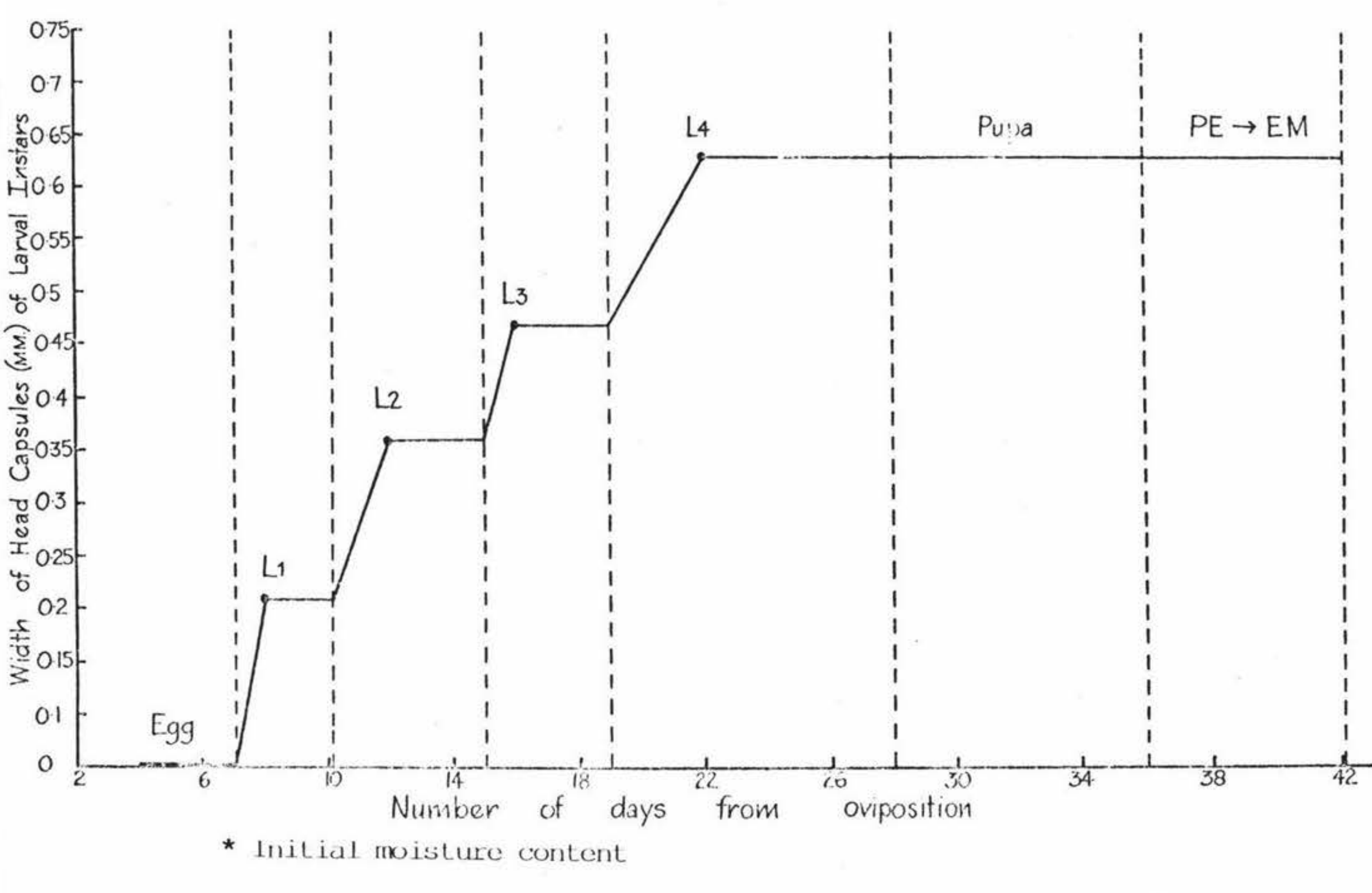


Figure 4.1: Development of Sitophilus oryzae from oviposition to emergence in rice of 12% IMC*

Figure 4.1.1: Development of S.granarius from oviposition to emergence in 12% rice IMC*



* Initial moisture content

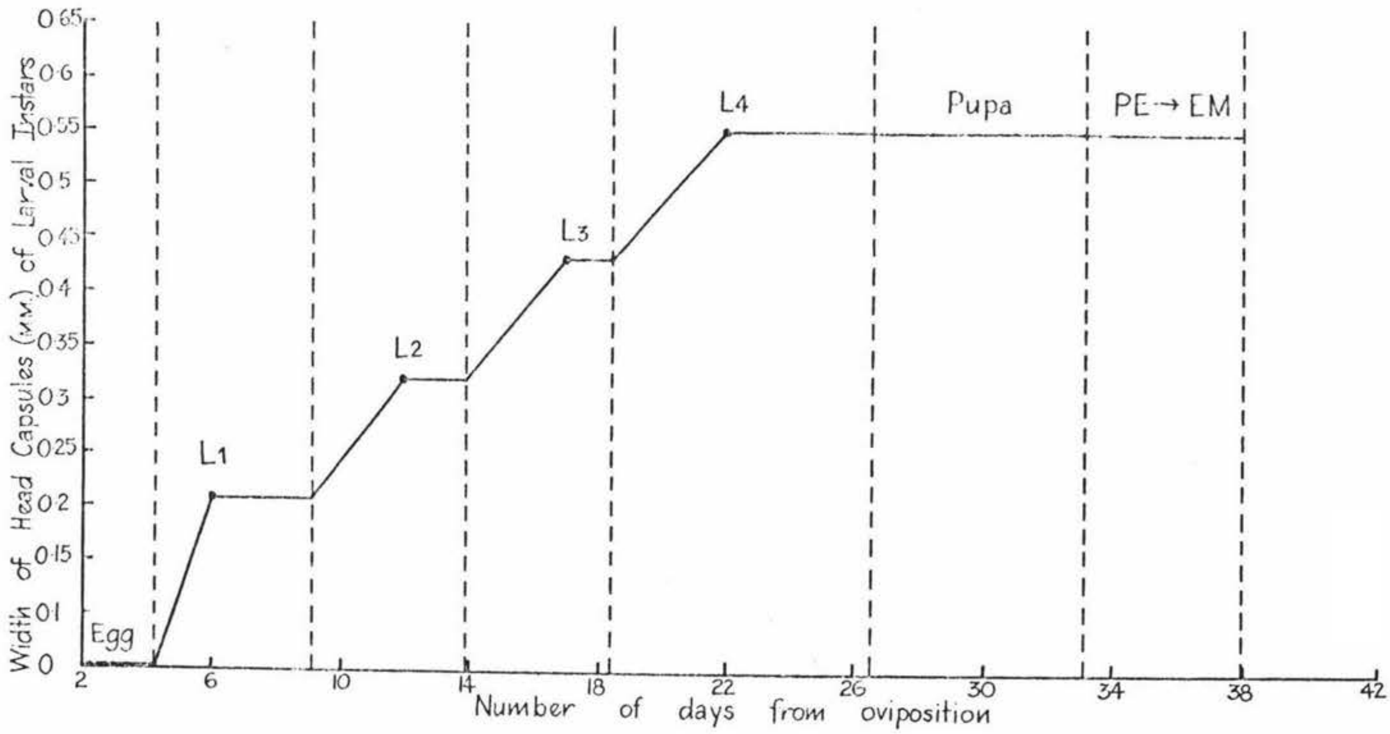
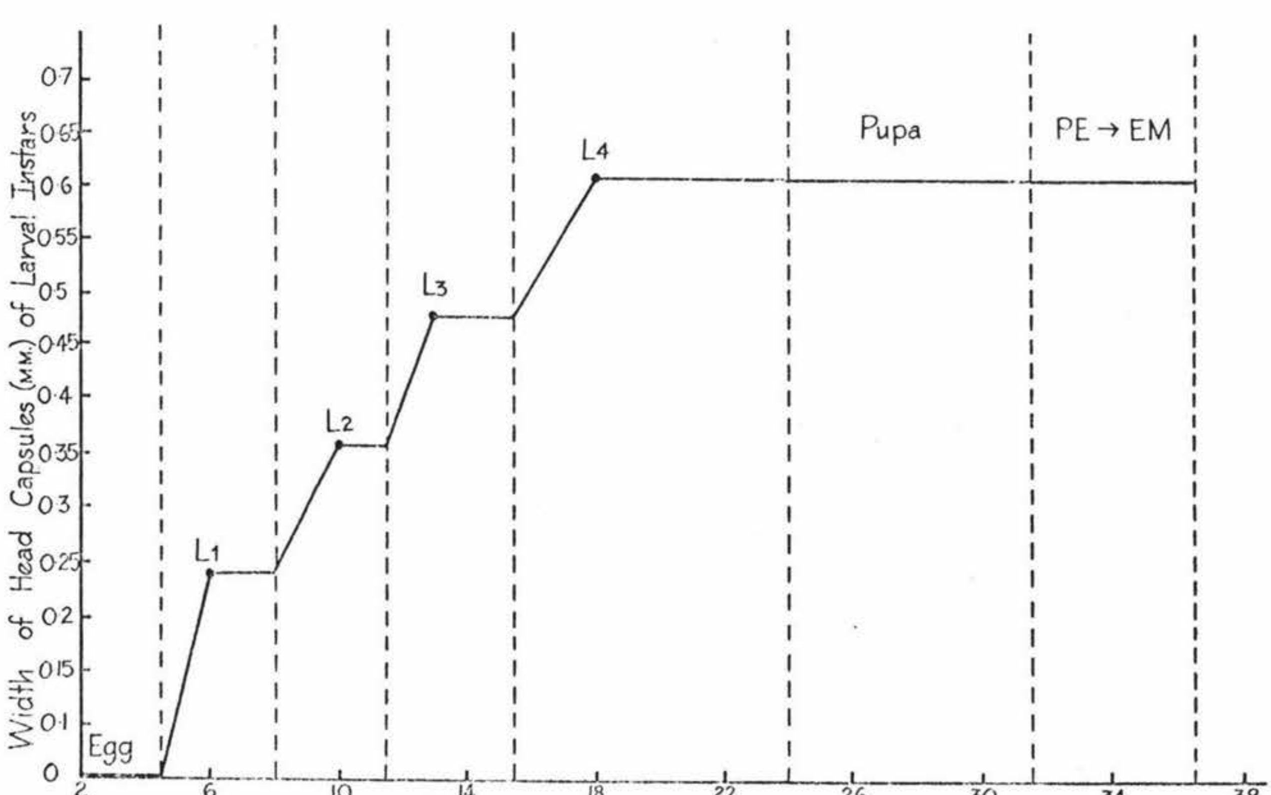


Figure 4.2: Development of S.oryzae from oviposition to emergence in 16% rice

Figure 4.2.1: Development of S.granarius from oviposition to emergence in 16% rice



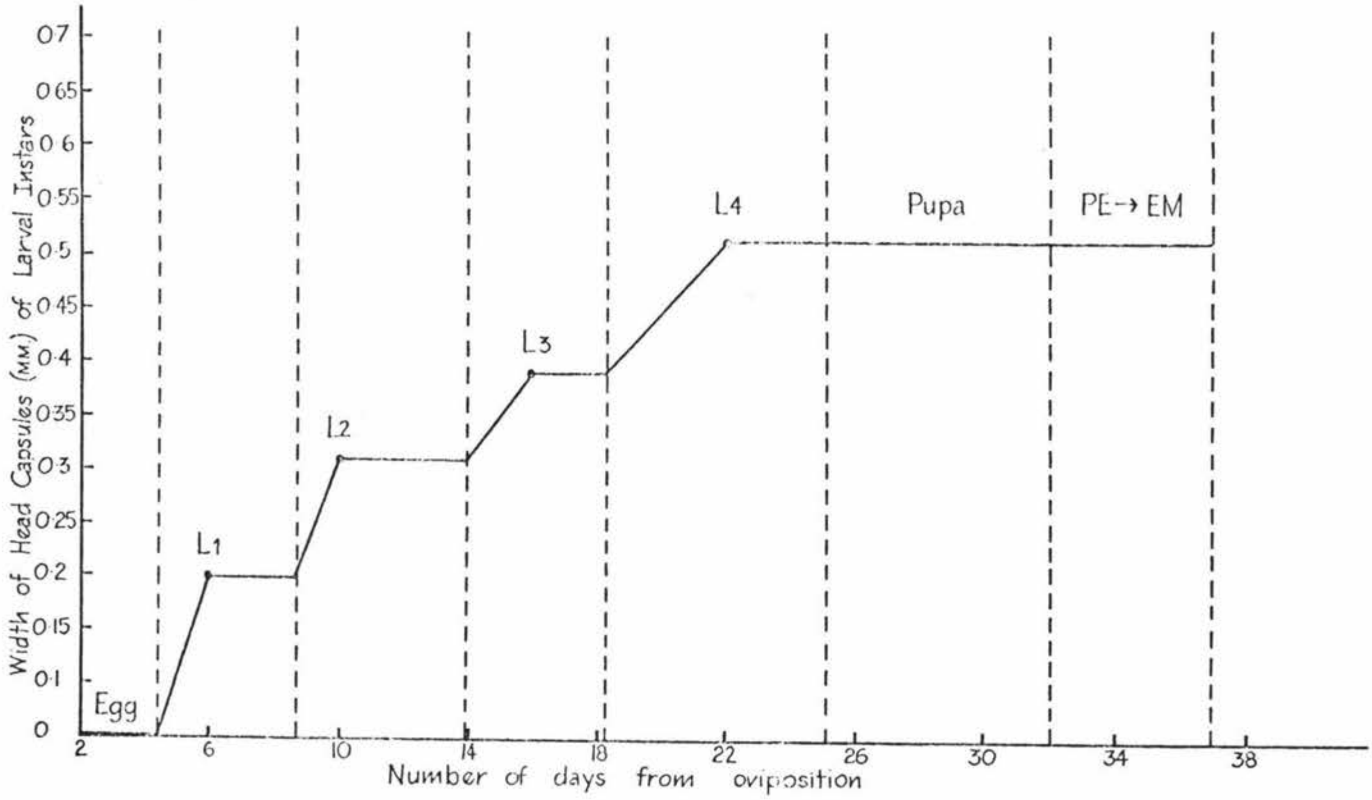
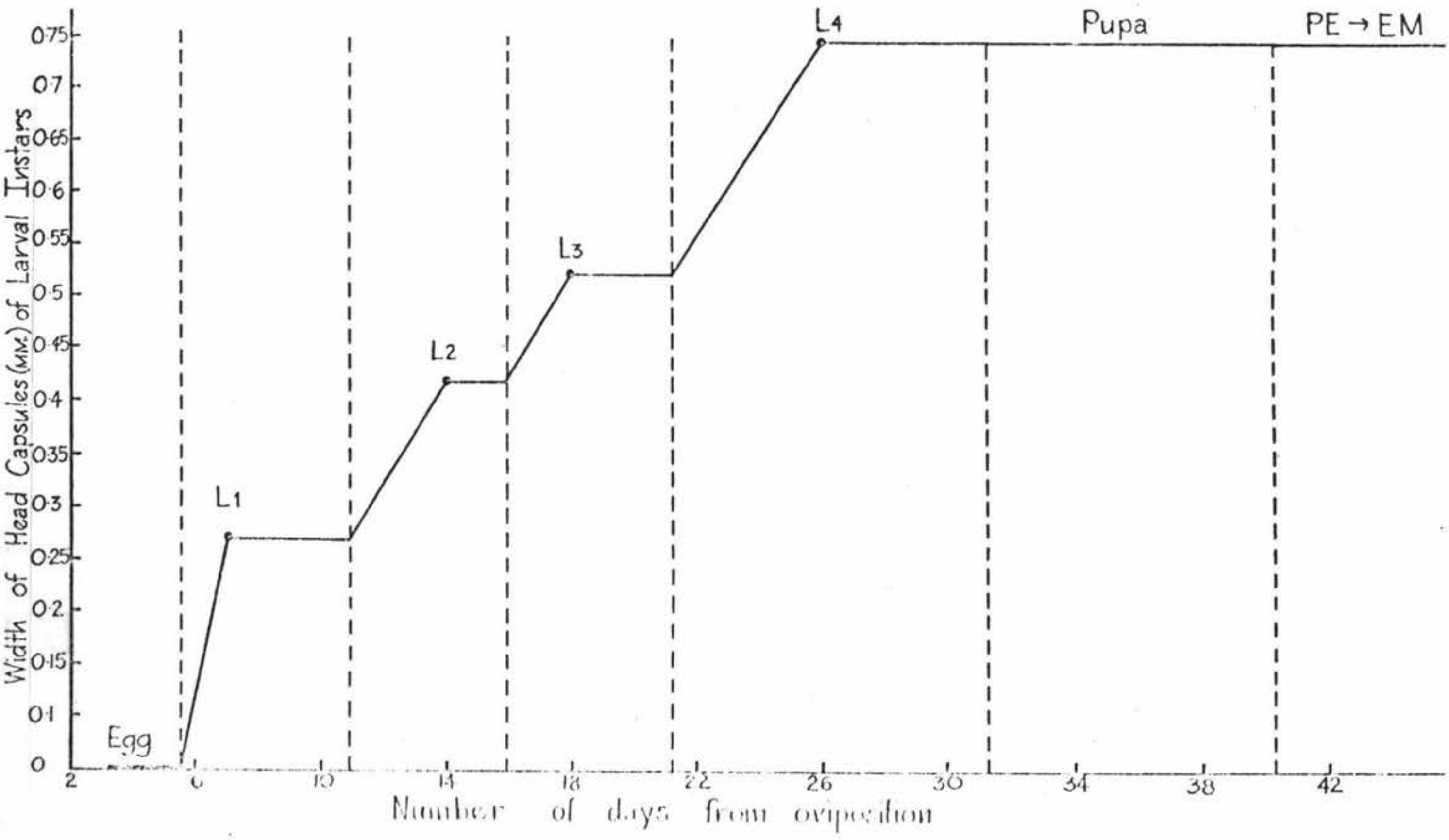
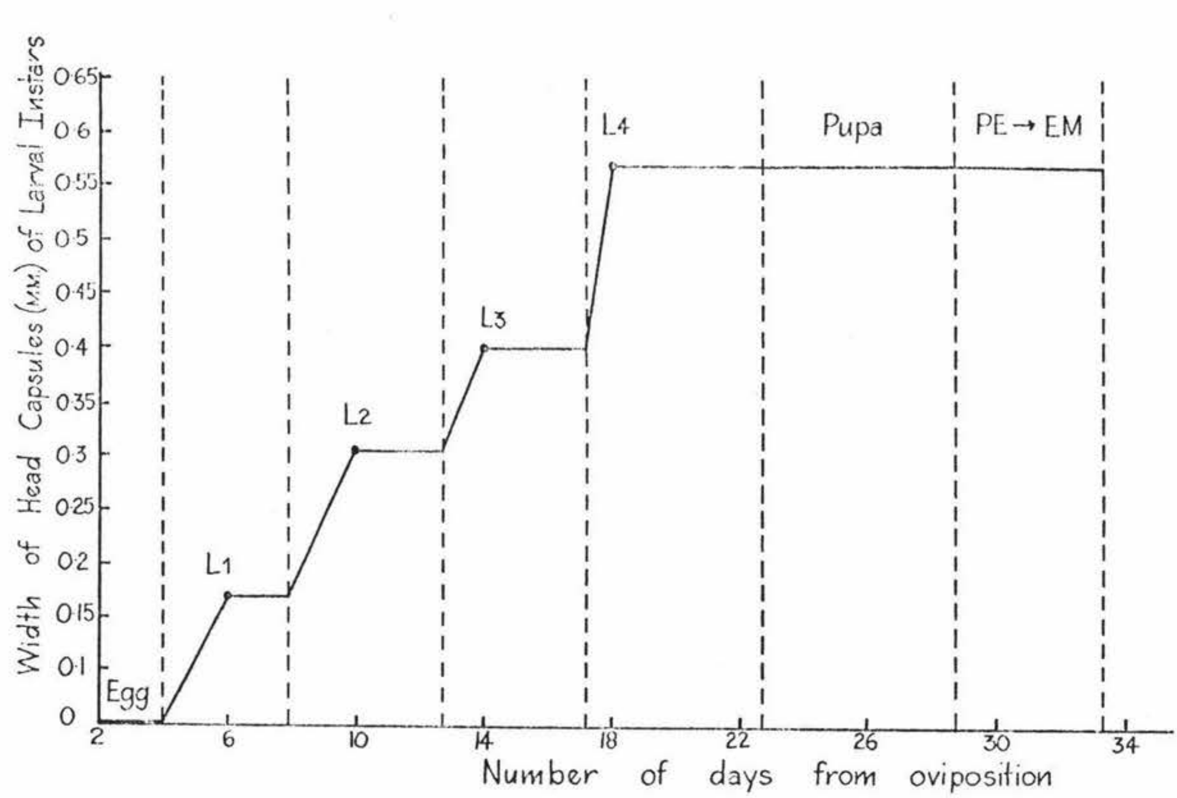


Figure 4.3: Development of S.oryzae from oviposition to emergence in 12% wheat

Figure 4.3.1: Development of S.granarius from oviposition to emergence in 12% wheat





<u>Figure 4.4</u>: Development of <u>S.oryzae</u> from oviposition to emergence in 16% wheat

<u>Figure 4.4.1</u>: Development of <u>S.granarius</u> from oviposition to emergence in 16% wheat

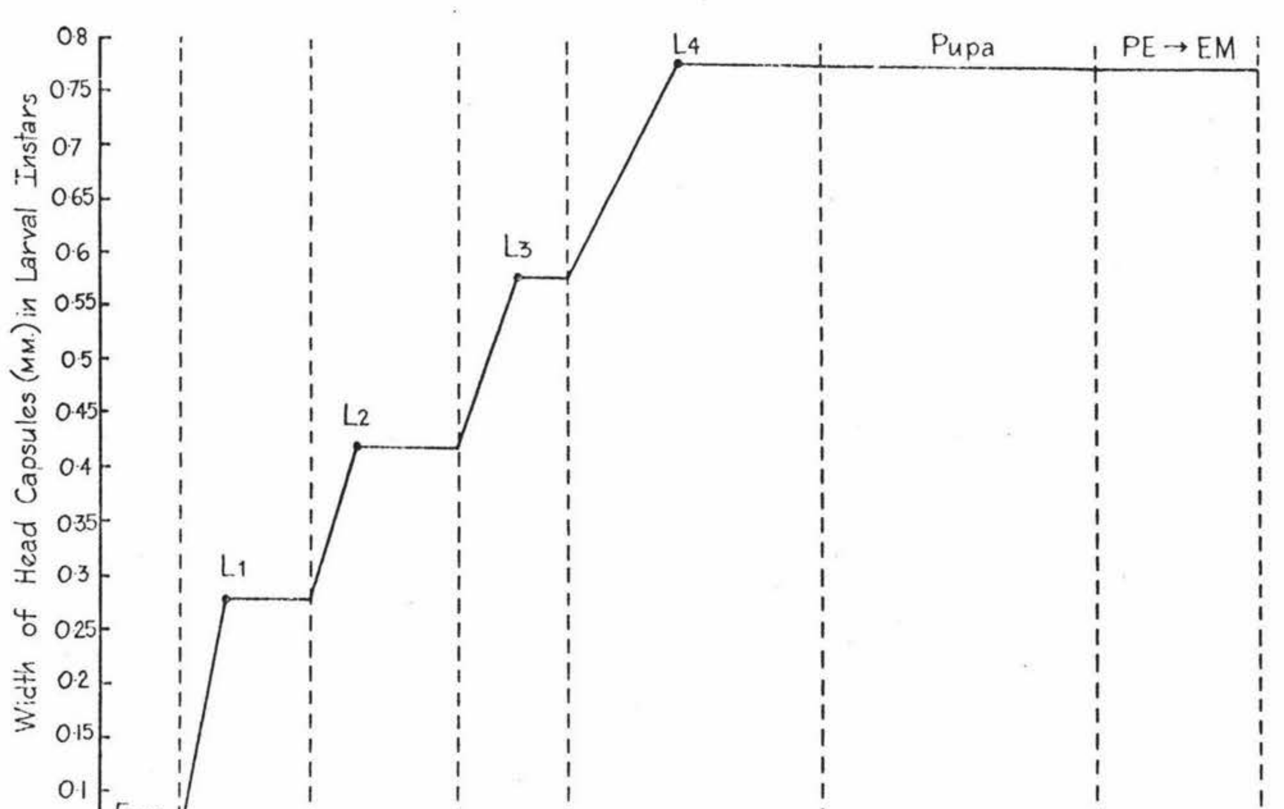


Table 4.1: Duration of developmental period for *S.oryzae* and *S.granarius* in wheat and rice of 12% and 16% moisture content

	Rice	Egg - Adult (days)	t		Wheat	Egg - Adult (days)	t
S.oryzae	12%	40.6 ± 1.3	0.43	S.oryzae	12%	36.9 ± 1.02	2.76 *
S.granarius		42.1 ± 1.7		S.granarius		46.8 ± 1.9	
S.oryzae	16%	37.9 ± 1.3	0.40	S.oryzae	16%	33.3 ± 0.7	1.41
S.granarius		36.5 ± 1.8		S.granarius		38.0 ± 1.8	
S.oryzae	12%	40.6 ± 1.3	0.81	S.oryzae	12%	36.9 ± 1.02	1.23
	16%	37.9 ± 1.3			16%	33.3 ± 0.7	
S.granarius	12%	42.1 ± 1.7	1.64	S.granarius	12%	46.8 ± 1.9	2.39 *
	16%	36.5 ± 1.8			16%	38.0 ± 1.8	

* Significant at 5% level.

4.4 Discussion

Although a great deal of work has been done on the duration of the egg, larval and pupal stages of Sitophilus under different environmental conditions, there is little published information on the effect of different food types and moisture levels on the duration of the various developmental stages. The whole developmental life is spent within one grain. The first-stage larva of Sitophilus requires a firm medium to be able to feed. Crushed grain or flour are not therefore suitable media.

The overall pattern of development was similar for the two Sitophilus species (Figs. 4.1 - 4.4) although the duration of each stage, as well as the total developmental time, varied slightly. As shown in Table 4.1, only in wheat of 12% moisture content was a significant difference found in total developmental period between the species with S.oryzae having a shorter developmental time than S.granarius.

Within the treatments using S.granarius, the developmental period was significantly longer in wheat of 12% moisture content compared with 16%. In rice, however, there was no such difference as mentioned in the results section.

Studies by Birch (1953) showed that within the range 12.5 to 15%, the effect of grain moisture content on developmental period is not very marked and he concluded that this factor could be ignored. This appears to hold good for the present data for S.oryzae and S.granarius only in rice. It is possible that wheat at 12% is relatively hard for the developing stages of S.granarius to feed on whereas the developing stages of S.oryzae are more adapted to feed through the harder grain. This result is in agreement with the results of Birch (1954) who found that S.oryzae had a greater capacity to increase in wheat which included lower immature mortality, shorter period from egg to adult, and shorter mean generation time.

Host suitability trials by Floyd and Newsom (1959) showed that S.oryzae has a feeding preference for unpolished rice over wheat. This is different from that preferred by the developing stages of the particular strain in the present study.

The present study showed a similarity to that of Eastham and McCully (1943) where the lower moisture conditions (water content of food) slowed down the development of Sitophilus granarius as a whole.

Kiritani (1965) considered only one set of environmental conditions, 30°C and 75% relative humidity, but he also included three types of grain: wheat, rice and maize. He found that irrespective of country of origin, all strains of S.oryzae matured more quickly in wheat than in rice or maize. Soderstrom and Wilbur (1966), however, found a degree of geographic variation in the length of the life cycle of S.oryzae and that the length varied with grain type, a finding similar to that of Singh et al (1974).

According to Eastham and McCully (1943) seed moisture levels have very different effects on the various stages of S.granarius. Although each stage and its duration were observed for both Sitophilus species in the present study, the effects of moisture levels upon each stage were not statistically analysed. Therefore, a summary from Eastham and McCully (1943) is given on the possible effects of moisture content of grain on the developmental stages of the Sitophilus species. In the case of the egg, moisture appears to have no significant effect. The four larval instars show a marked reaction to humidity though the effect is least in the first larval instar. The pupa behaves in the same way as the egg. Moisture content and humidity had little or no effect on the duration of the embryonic or pupal phases though low humidity tended to delay the hatching of the egg.

The egg and pupa are subjected only to atmospheric relative humidity whereas the larva, being a feeding phase, is subjected both to atmospheric humidity and to food moisture content. The embryo and pupa favour the evaporation of water while the larva needs to retain water to incorporate into its own tissues. The varying moisture contents of rice and wheat in the present study may tend to induce different states of dessication in the insect and these in some way may retard development to a degree as seen for S.granarius in 12% wheat. Kono (1960, unpublished) found that variation in body size was associated with a parallel change in the duration of development; the larger race required a longer time for its development than the smaller race. S.granarius is larger in size than S.oryzae and this could explain why the development of S.granarius from egg to adult takes a longer period.

Most of the workers studied development of Sitophilus species using wheat as the most favourable food medium, although Kiritani (1965) had quoted Kono's (1960 and unpublished) findings involving three types of grains (wheat, rice and maize) and confirmed that S.oryzae developed faster on wheat than on rice. Baker and Mabie (1973b) showed that pupation and adult eclosion of S.granarius took considerably longer time than the other species. This also appeared to be a major factor in the present study.

Table 4.2 shown below summarises the mean duration of developmental period found by the named authors. All the authors chosen have used the same optimum relative humidity of 70% and where temperature used was slightly different from 25^{O}C it is stated so in Table 4.2.

Table 4.2 shows that each author has found somewhat different values for mean development period from egg to adult for S.oryzae and S.granarius. Satomi (1960) who studied S.oryzae and S.zeamais from several parts of the world, over a range of temperatures found differences up to 10% in the duration of the developmental period. Evans (1977a, b) also found variations of up to 10% in the length of the immature phase of both S.granarius and S.oryzae from a range of sites in Australia. He also found significant differences between these

Table 4.2: Summary of results obtained by other authors for the total developmental period for S.oryzae and S.granarius at 25^{o}C and 70% R.H.

Author(s) and Year	S.oryzae (egg - adult) days	Grain	S.granarius (egg - adult) days
1. Eastham & McCully (1943)	-	wheat	35
2. Birch (1945a)	34.1	wheat	-
3. Birch (1945c)	12% 39.9	wheat	-
	14% 34.3	wheat	-
4. Richards (1947)	-	wheat	45
5. Eastham and Segrove (1947)	-	wheat	12% 40
	-	wheat	16% 35.5
6. Khan (1949)	36	wheat	38
7. Reddy (1950)	33	wheat	-
8. Howe (1952)	32	wheat	-
9. Kono (1960 and unpublished) [30^{o}C]	25	wheat	-
	27	rice	-
10. Soderstrom (1960)	25	wheat	33
11. Kirkpatrick (1962)	-	wheat	44
12. Surtees (1965)	36.6	wheat	-
13. McFarlane (1968)	34	wheat	-
14. Golebiowska (1969)	32.7	wheat	-
15. Sharifi and Mills (1971)	37	wheat	-
16. Sharifi (1972)	31	wheat	-
17. Ungsunantwiwat and Mills (1979)	34.2	wheat	39.5

populations and others from Britain and Canada (Evans, 1979a).

The effect of parental age upon the duration of the developmental period was not considered in the present study.

CHAPTER FIVE: POPULATION GROWTH OF S.ORYZAE AND S.GRANARIUS IN SINGLE AND MIXED CULTURES

5.1 Introduction

Species with similar requirements compete for a certain set of necessary resources and with evolutionary time there tends to be a divergence of exploitation patterns and sub-division of resources. Refuges from competition develop so that coexistence is possible (Price, 1975). Thus, a certain number of species become packed into the same community depending on the resources available and how they are subdivided by organisms present.

A primary objective of the present study was to explore and describe what happens when two closely related species of grain weevils, Sitophilus oryzae L. and Sitophilus granarius L. are placed into direct competition in a shared environment to which both are individually well adapted. Sitophilus species seem particularly favourable for research of this type as much is already known about their population behaviour in a whole grain environment. Park (1948) suggested that there was more validity in using two species of the same genus instead of selecting forms of greater taxonomic divergence. This was also recognised earlier by Charles Darwin who wrote (The Origin of the Species):

> As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera.

If the existence of interspecies competition is proved, Park (1954) suggested the need to describe empirically the "end-result" of such a competition for a defined set of conditions, as in the present study.

5.2 Materials and methods

5.2.1 Insects

One hundred unsexed adults of Sitophilus granarius and Sitophilus oryzae approximately two weeks old were used in the single species treatments. The adults were carefully screened to ensure pure single-species populations.

In the treatments with mixed populations, 50 Sitophilus oryzae and 50 Sitophilus granarius were selected at random from culture and placed into one treatment.

5.2.2 Grain

The preheat-treated whole wheat grain, with initial moisture contents of 12% and 16% was used. As grain is hygroscopic, the initial seed moisture content undoubtedly changed over the course of these experiments until it reached equilibrium with the storage environment of 70% R.H. (at 25°C). These possible changes were not monitored. As the equilibrium moisture content of wheat and rice at 70% R.H., and 25°C is between 14 and 15% (M.J. Hill, personal communication) the initial moisture content of 16% is unlikely to have been decreased greatly but the initial moisture content of 12% may well have been raised with time, particularly where insect populations developed and additional moisture may have been generated. In order to provide enough grain for food and oviposition for 18 weeks, 3000 grains of wheat were put in each treatment. This was repeated using unpolished rice grains.

Half litre glass jars with screw top ring covers were used in this experiment. These jars could not be sealed due to the prolonged period the insects and grain had to be in the jars, but care was taken to ensure there was no contamination during the experiment.

Therefore, the rings were fitted with 0.5mm wire gauze. Beneath the wire gauze, filter paper was also fitted, in order to prevent fungal spores and mites from entering. For 18 weeks the treatments remained mould and mite free.

5.2.3 The experimental design

One hundred weevils of each species and 100 weevils of mixed weevils were allowed to oviposit in 3000 grains of wheat and rice each at 12% seed moisture content. The same number was placed on grains at 16% SMC. The treatments had four replications. The oviposition period allowed was four days, after which the weevils from all the treatments were sieved off. The treatments were kept in controlled environment cabinets.

The sampling regime consisted of sieving the grain, counting adults, if any, and weighing the dust. The grain and adults were returned immediately to the jars. There was minimum disturbance to the developing larvae. The first adults emerged after eight weeks and the second generation also took eight weeks to develop. Three samplings were carried out. Each sampling of 48 jars took about two weeks to complete.

The treatments were held at 25^{o}C and 70% R.H. in a Warren-Sherer cabinet. The cabinet had temperature and humidity regulators which needed care in their use. In order to increase the relative humidity of the cabinet to 70%, glycerine mixed with water in the proportion of 55% to 45% in a tray, was first kept in the cabinet. This, however, was not effective. After several trials, the most effective means of maintaining the R.H. at 70% was to allow water to flow in drops along the side of the cabinet. The relative humidity and temperature were monitored daily to ensure that conditions were stable.

This study was aimed at ensuring that competition took place in the mixed populations in the second generation. During the sampling of mixed populations, the adults were identified, numbers of each species alive and dead were recorded, as well as the weight of the dust.

The experiment was terminated at 25 weeks when condensation killed the weevils in some treatments and caused extensive mould growth in others.

5.3 Results

Population development of Sitophilus oryzae and S.granarius in single and in mixed culture of the two species took different forms. The population development of each species is plotted on the logarithmic scale (Figs.5.1 - 5.4).

In single species culture, S.oryzae multiplied faster than S.granarius under all conditions. Since 100 adults of each Sitophilus species were introduced, allowed to oviposit and then removed, the initial number of eggs laid could not be estimated. However, under each of the conditions in single species culture, S.oryzae numbers increased to over a thousand after 25 weeks except in rice of 12% moisture content where the population reached 372. The patterns of increase were slightly different between rice and wheat. In rice, there was a sharp increase over the first generation (up to 17 weeks). From weeks 17 to 25 the rate of increase was less (Figs.5.1 and 5.2 for S.oryzae single species only).

In wheat, the pattern was similar as in rice for the first two generations but then there was a further sharp increase during the third generation (from 17 weeks - Figs. 5.3 and 5.4). These patterns were similar for both moisture contents.

The patterns of population increase for S.granarius in single cultures were quite dissimilar according to treatment and overall, the total increase of S.granarius was much less than that of S.oryzae. As with S.oryzae in 12% rice, S.granarius gave rise to only small numbers of progeny of 102 (Fig. 5.1) compared with the other treatments. Twelve percent wheat (Fig. 5.2) seemed to provide the most favourable conditions for this species. In 16% wheat, S.granarius reproduced initially in low numbers but after 17 weeks there was a sharp increase.

S.oryzae in single species culture reproduced in greater numbers in wheat with 16% moisture content compared with 12%. In rice, they also did better in 16% than in 12%. Single species culture of S.granarius in rice also showed more progeny at 16% than at 12% moisture content. However, in wheat, 12% moisture content produced higher numbers than 16%.

In mixed cultures the patterns of population growth for each species of Sitophilus were similar to those of single culture under some conditions but markedly different under other conditions. Thus in 12% moisture content wheat the patterns of population growth for both species were closely similar in mixed compared with single culture (Fig. 5.3) with only a slight indication of a lower rate of increase in mixed culture. This contrasted strongly with the situation in 16% wheat where S.oryzae numbers were slightly less in mixed culture but where S.granarius actually performed better in mixed cultures compared with single (Fig. 5.4).

In 16% rice there was little difference between single and mixed cultures for S.oryzae but S.granarius performed very poorly in mixed culture (Fig. 5.2).

The most striking result perhaps was obtained in 12% rice (Fig. 5.1). Here the population growth of S.oryzae was considerably less in mixed culture than in single but under these conditions S.granarius was almost totally suppressed, with only three offspring produced after 25 weeks.

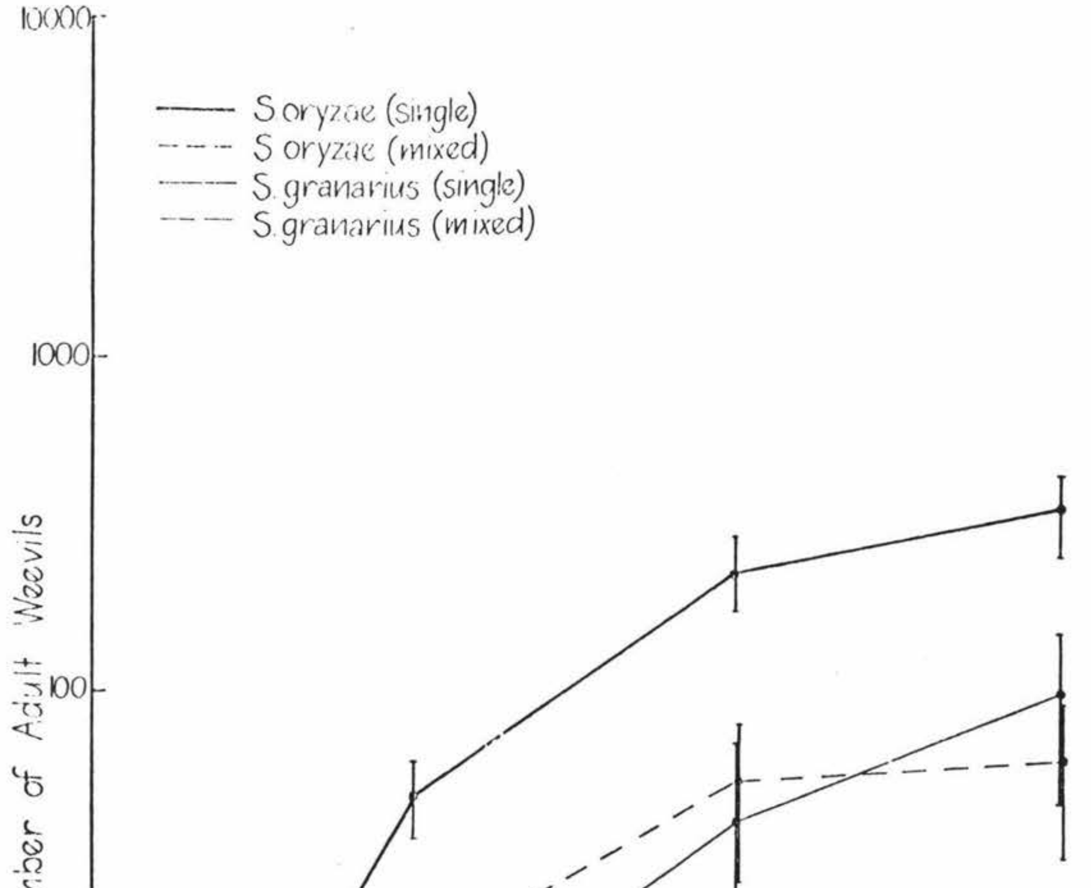


Figure 5.1: Population growth of S.oryzae and S.granarius in single and mixed cultures in 12% rice IMC. Vertical bars represent the S.E. of the mean.

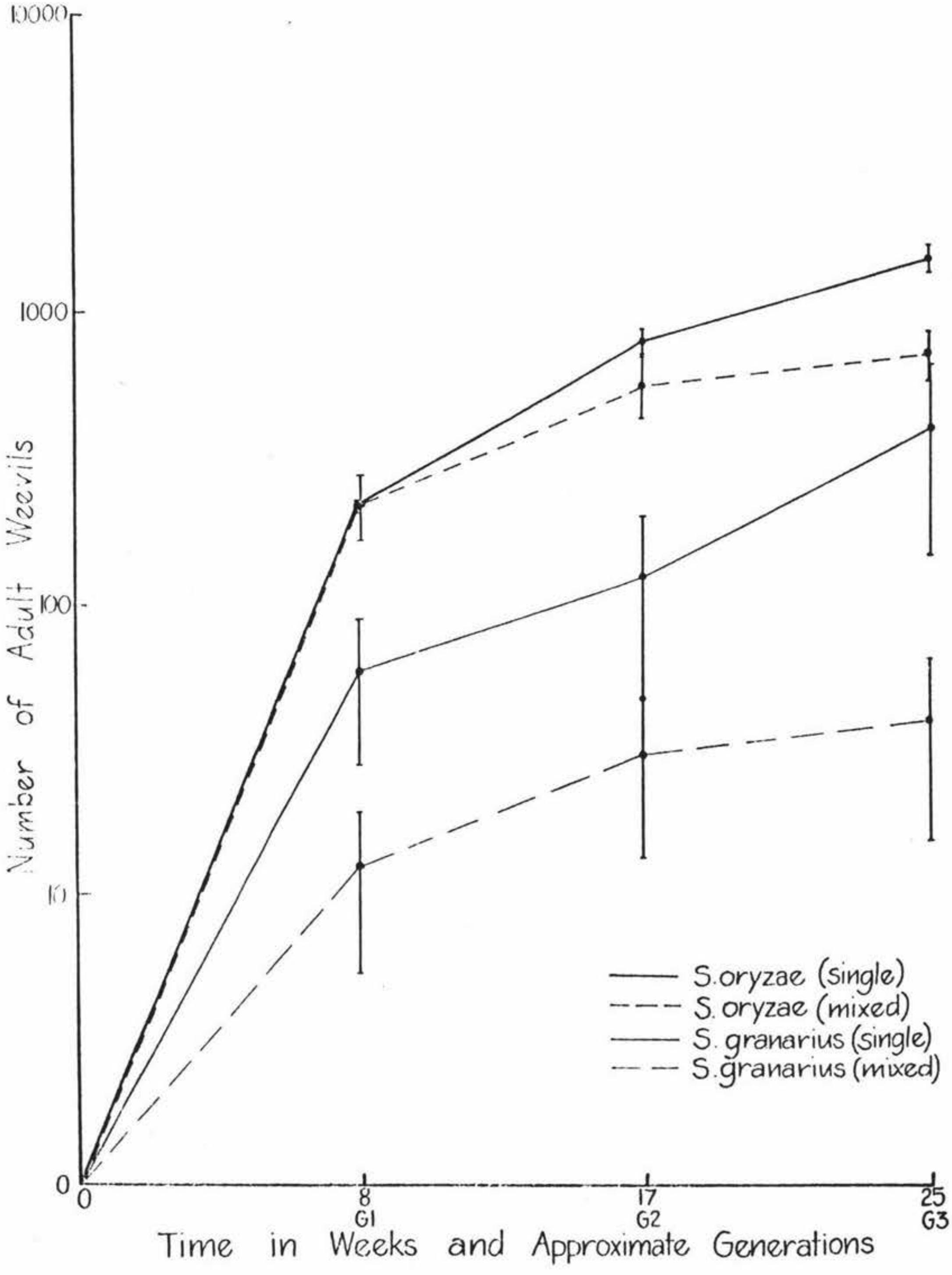


Figure 5.2: Population growth of S.oryzae and S.granarius in single and mixed cultures in 16% rice IMC. Vertical bars represent the S.E. of the mean.

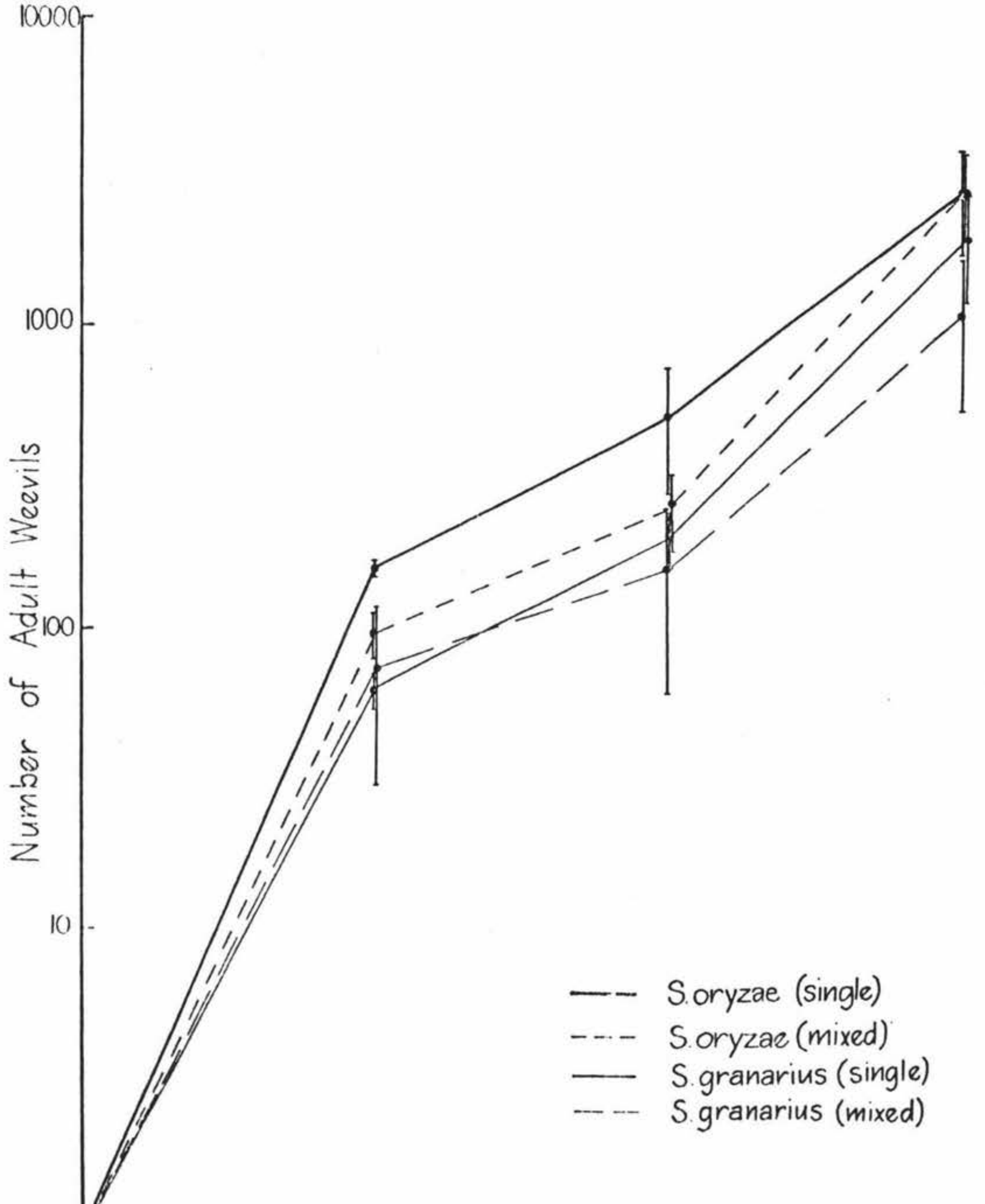


Figure 5.3: Population growth of S.oryzae and S.granarius in single and mixed cultures in 12% wheat IMC. Vertical bars represent the S.E. of the mean.

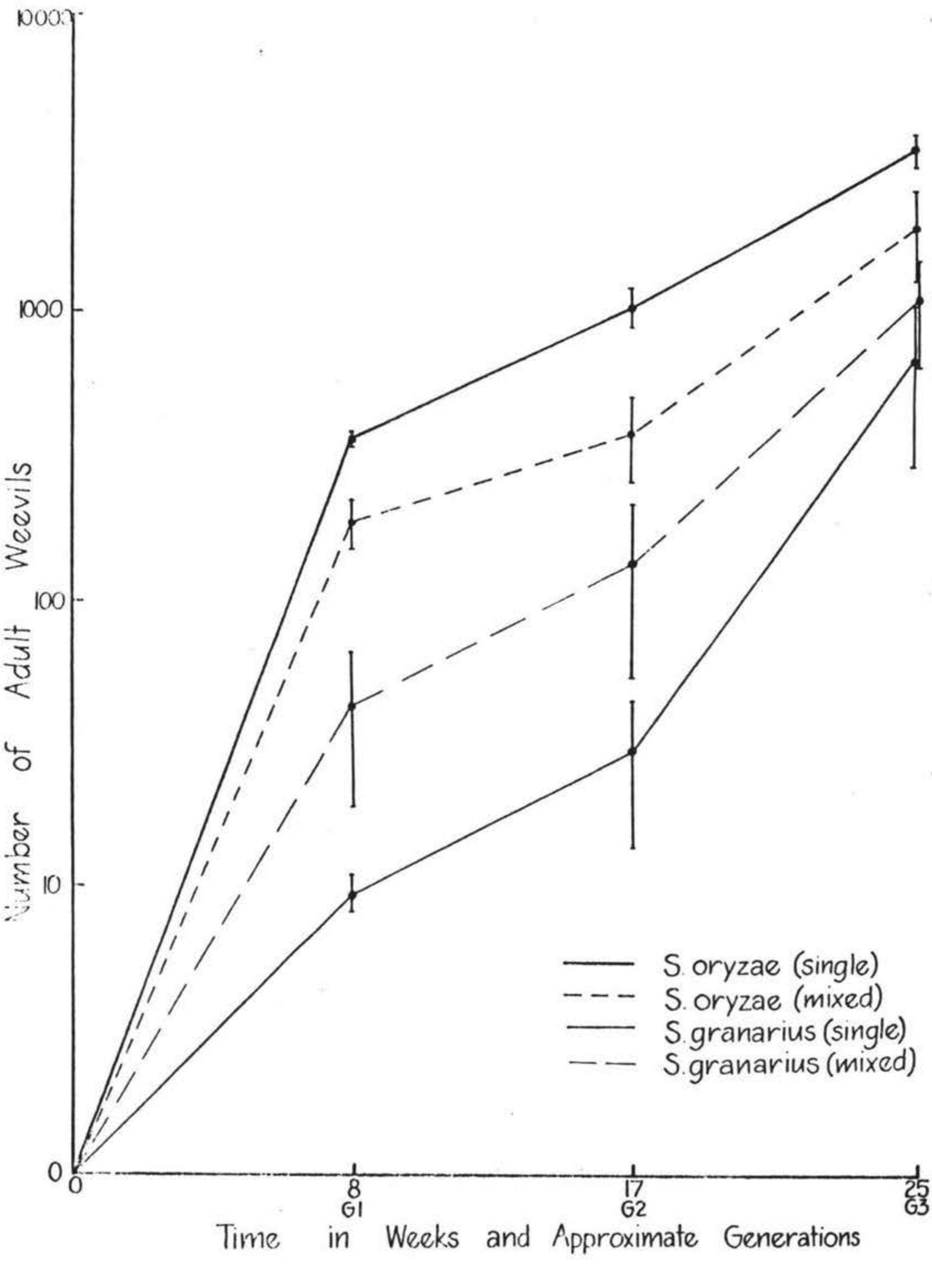


Figure 5.4: Population growth of S.oryzae and S.granarius in single and mixed cultures in 16% wheat IMC. Vertical bars represent the S.E. of the mean.

5.4 Discussion

Under all conditions (grain species, moisture content) of single species cultures, Sitophilus oryzae was more productive than S.granarius and more so in wheat than in rice.

Unlike population interaction studies undertaken by earlier workers on mixed species of insects where one species always ousted the other, in the present study the two Sitophilus species existed together while still increasing to vast numbers by the 25th week, except in rice of 12% moisture content where S.granarius was virtually eliminated at the end of 25 weeks. In this same treatment, S.oryzae having increased by nearly three times between weeks 8 and 17, produced only a further 10 individuals by 25 weeks. A similar effect was noticed in an experiment of Ciesielska's in 1975. He suggested that it was due to competitive action exerted by the other species, i.e. by S.granarius in the present study.

As Coombs and Woodroffe (1963a) have pointed out, it is unlikely that successive species dominance can be explained from results of single species laboratory experiments. It seems that the explanation will prove to be complex, determined by interactions between the species and the environment (Coombs and Woodroffe, 1973). The species used by Coombs and Woodroffe in competition experiments were not closely related, whereas the present study involved two species within the genus Sitophilus. Therefore, it is not possible to compare the results of the present study with those of Crombie (1942), Park (1954), Coombs and Woodroffe (1963a, b; 1973), Ciesielska (1972, 1975), or Ayertey (1979). There is no previous published information on interactions between Sitophilus oryzae and S.granarius with which to compare the present results.

There are several ways in which species can share resources for as long as the habitat remains relatively unchanged. Not all of them involve competition (interaction between two species which results in reduced population size of both competing species [Pontin, 1982]) and therefore it is important to provide evidence of a population reduction to establish that competition is taking place. If Pontin's (1982) definition of interspecific competition is taken into consideration, the mixed species of the present study do exhibit competition since the population size of both competing species was reduced. However, Pontin has not defined by how much populations should be reduced before they qualify to be in competition. In the present study for instance, the populations of mixed species were reduced considerably (compared with single species numbers) in 12% and 16% rice (Figs. 5.1 and 5.2), whereas, in 12% wheat there was only a very small decrease and in fact, S.oryzae numbers in the mixed culture finally reached similar numbers to single species culture (Fig. 5.3).

Although there was slight reduction in numbers of S.oryzae in mixed cultures compared with single in 16% wheat (Fig. 5.4), S.granarius in this mixed culture completely outperformed that in single species culture. This unique feature did not occur in any other treatment in the present study.

Lotka (1925) and Volterra (1926 - translated in Chapman, 1931) stated that the results of competition between two species may be any of three possibilities:

1) Species A always displaces B or vice versa.
2) Instability with displacement of either by the other depending upon starting density and other factors.
3) Stable coexistence resulting from each species limiting its own increase.

Comparing this concept with that of Darwin, that intraspecies competition is generally more severe than interspecies competition, Pontin (1958, 1961) and Cole (1960) suggested that stable coexistence with continuous competition is of frequent occurrence. Because of the relatively short period over which the present experiments were run it is not possible to say with certainty which final end result would have eventuated under the various conditions employed. There is much speculation and literature about competition between populations which are brought into tension with each other through their respective demands upon an environment shared by both but limited in potentialities for exploitation. This will be discussed in the next chapter.

CHAPTER SIX: GENERAL DISCUSSION AND CONCLUSIONS

In this final chapter attention is focussed first on populations of Sitophilus oryzae and S.granarius reared separately as single species systems. Discussion then moves to interspecies systems in which competition between the two species has been shown to occur. Finally, the relevant literature on competition is considered in relation to the results of the present study.

In single species cultures, the patterns of population growth over three generations for each species were generally consistent with the results obtained from separate studies to determine fecundity, longevity and rate of development from egg to adult emergence. In such studies S.oryzae had a higher fecundity and faster rate of development than S.granarius although longevity was somewhat less. The latter was obviously insufficient to compensate S.granarius for lower values in the other factors as this species was consistently outperformed by S.oryzae under all experimental conditions when cultured over three generations.

A peculiar feature of the results of population growth was the reduced growth rate in the third compared with the first generation for both species in rice. The effect was more marked for S.oryzae than for S.granarius and occurred in both single and mixed cultures. It was not, however, apparent in cultures on wheat. Such an effect is not readily explicable in terms of competition unless rice provides a more limited resource than wheat. Accumulation of toxic waste products is another possible explanation but again does not account for the difference between rice and wheat. Park and Woollcott (1937) showed that highly conditioned (used for culture of the species) flour reduced fecundity, increased variability of egg production and increased duration, variability and mortality of larval stages.

The results obtained on oviposition rates (Chapter Three) show distinct periodical fluctuations for both Sitophilus species.

These fluctuations were more pronounced for S.oryzae than for S.granarius. The most likely cause of these fluctuations is periodicity of ovarian development and hence of egg production. They were marked in the present experiment because all adults used were newly emerged. In populations of weevils allowed to develop over several generations any such periodicity in oviposition would be smoothed out as generations overlap and the adult population becomes widely mixed in age.

The lower rates of fecundity observed in lower moisture content grain are probably due to the relative hardness of the grain and the consequent greater difficulty in excavating a cavity for egg deposition (Davey, 1964; Russell, 1968). It is possible, however, that greater larval mortality in lower moisture content grain (and hence lower estimate of eggs laid) may also have occurred. Richards (1947) has pointed out that reduction in oviposition rate of Sitophilus may also be due to "instability" of the grain mass and that stability is increased by increased bulk of grain. Howe (1952) considered that depths of grain of less than 7cm discouraged egg laying by S.oryzae. He also found that close grouping of females further reduced egg output. Both factors could be relevant to the present study. Pearl (1927) has pointed out that fecundity is one of the two key biological variables involved in population dynamics (the other being mortality) so that any factor affecting fecundity must be regarded as important in overall population development. In mixed species cultures S.granarius was much more severely affected than S.oryzae except in wheat of 12% initial moisture content, where there was little difference. In contrast however, the most severe depression of S.granarius occurred in 12% rice. It appears that S.granarius is more sensitive to competition when environmental conditions are more severe.

Although S.granarius was in general more severely affected in mixed culture than S.oryzae there clearly were reciprocal effects in that S.oryzae did not perform as well in the presence of S.granarius as in its absence.

An unusual feature of the mixed culture results was the better performance of S.granarius in mixed culture in 16% wheat compared with single species culture under the same conditions. No explanation can be offered for this although Ciesielska (1971, 1972) has stated that stimulation of the growth of one species commonly occurs simultaneously with inhibition of the competing species. In the present instance however, S.granarius was not the most successful species. It simply did better in the presence of S.oryzae than in its absence, while the latter was unaffected. Ayertey (1979) in studying the growth of single and mixed populations of Sitophilus zeamais and Sitotroga cerealella on starch maize found that S.zeamais reached greater numbers in mixed populations than in single. He also could not suggest an adequate explanation.

According to Park (1954), two types of behaviour may cause competition between species and these components are:

1) 'exploitation' (individuals of different species are observed to use some of the same resources)
2) 'interference'(where fighting or other directly damaging behaviour occurs).

Pontin (1982) elaborates in detail the effect on population size when either one of the above components occurs or a combination of both. Park (1954) stressed that although these may be different as processes, they must often affect each other. Exploitation probably best describes the processes in the present study except in the case of S.granarius in mixed culture in 12% rice when this species was severely depressed. In this case, interference may well be involved whereby the shared resources are indivisible and where one species (in this case S.oryzae) prevents the other from taking its share. The outcome may be decided by direct aggression (which was not observed in the present study) or simple avoidance of a dominant individual by a subordinate one (Pontin, 1982). Individuals of one species interfere with individuals of another species by using a wide variety of behaviour. The result may sometimes be mosaic distributions or sharpened zonal boundaries between species (Pontin, 1982). This was not investigated in the present study.

Priority of access to resources is the usual result of interference between individuals of mobile species (Pontin, 1982).

Morse (1974) refers to this priority as 'social dominance'. He also has suggested that it is often not easy to state which species is consistently dominant to another. Perhaps if the competition experiments in the present study had been allowed to progress for a longer period, there may have been a change in the relative abundance of the species. This could apply particularly to 12% wheat where both species at the end of 25 weeks numbered about one thousand. Individual variation in age and size or changes in environmental factors may reverse the direction of dominance (Pontin, 1982). Closely related species are not necessarily more likely to displace each other than distantly related species and displacement could be rendered less likely if closely related species are similarly affected by those factors which cause changes in numbers and which might otherwise be expected to cause departure from equilibrium proportions (Pontin, 1982).

Environmental factors which influence population levels and mechanisms through which they act are of primary importance to the present study. The literature indicates that the subject has been approached from two viewpoints. One viewpoint is primarily mathematical; the other based on observational data with conclusions reached through philosophising on the results. The present thesis fits into the second category.

Chapman (1933) has pointed out that population trends are determined by the rate of reproduction on the one hand and by the "resistance" of the environment on the other. Studies of oviposition rates of both insect species in the present study do to a considerable extent explain the trends in populations. For example, low oviposition rates for both species in 12% moisture content rice corresponded to the lowest population development in the population experiments. Chapman (1933) also found that low populations produced as a result of low egg-laying rates involved daughters who had inherited their mothers' reduced egg-laying capacity. A selection process over several generations is implied in such a finding. Over the comparatively short (three generations) duration of the present study such effects seem unlikely.

In general in the present study, both species of Sitophilus gave rise to higher populations in wheat than in rice. This suggests that wheat for this insect is more nutritious than rice or that competition in some way is less in wheat compared with rice.

Chapman (1928) showed that under controlled conditions, Tribolium populations came to a point of saturation and then maintained this level with only minor fluctuations. This was regardless of whether the population was low or high at the beginning of the experiment. Similar results were also reported by Sweetman and Palmer (1928). Milne (1957, 1962) considers intraspecific competition to be the "one and only perfect density-dependent factor" which prevents populations increasing to the point of collective suicide when the ultimate capacity of the environment is exceeded. It is unlikely that such a point had been closely approached in the present experiment, though population growth had slowed considerably in the third generation compared with the first for both species in single and mixed culture in rice.

The study of individual components of population growth (fecundity, adult longevity, rate of development from egg to adult) are clearly valuable in predicting initial rate of increase of a species in single species culture, but offer little in the way of explanation of the outcome once competition effects start to become important. This applies to an even greater extent to mixed species cultures where interspecific competition may be important from the outset.

Crombie (1945, 1946) performed extensive, though simple, experiments with grain beetles in cultures. The most illuminating series of these concerns Tribolium confusum and Oryzaephilus surinamensis. Both of these species are depressed in numbers by the presence of the other and Oryzaephilus is the worst affected of the two, a situation very similar to that of the two Sitophilus species in the present study. In Crombie's experiments there was no question that the species were in competition. Stability in the system was attained by the emergence of an equilibrium mixture of the two species. In the present study there was no evidence that such an equilibrium was reached, probably because of the limited duration of the experiments.

Pontin (1982) has pointed out that there may be many differences between species which improve stability of mixed populations because they reduce the frequency of meetings between individuals of different species. This reduces interference and promotes coexistence even though the species still share the same food. Superabundance of resources is usually considered to be important for coexistence but if such factors are operating to permit stable coexistence, superabundance of resources becomes irrelevant.

The techniques employed in this study could in some ways have been improved. The choice of Sitophilus species for example meant that oviposition could not be estimated directly, neither could mortality of larval stages be examined because of their internal situation within grains. Tribolium species would have been more suitable in both respects as eggs and larvae occur freely within the storage environment. Tribolium species are, however, more difficult to distinguish than the two species of Sitophilus used.

In the experiments involving population growth over three generations, it might have been possible to mark the adults of the first generation as they appeared so that they could have been distinguished from those arising later. This could then have provided more detail on the components of population change in these cultures.

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