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FOOD QUALITY, DIET AND REPRODUCTION OF HOUSE MICE ON IRRIGATED CEREAL FARMS

by
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A thesis submitted for the degree of Doctor of Philosophy, in the Australian National University

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Declaration

This thesis is my own work, except where specifically acknowledged.

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ABSTRACT

Breeding in field populations of house mice (*Mus musculus* L.) is usually seasonal, and this has often been attributed to seasonal fluctuations in the quality or abundance of food. Populations of house mice in Australia are subject to irregular outbreaks, and previous authors have suggested that these 'plagues' are causally linked to improved breeding which occurs when food supplies are temporally improved by unusually favourable weather. This thesis examines the link between breeding and the quality and abundance of food supplies in the Murrumbidgee Irrigation Region, NSW, an area where plagues have occurred in the past. The research involved a combination of descriptive investigation, laboratory experiments and field experiments.

Available seeds were monitored in six habitats on two cereal farms. Because of rotational cropping and irrigation, seeds were available in different habitats in different seasons. In all habitats mice were mainly granivorous and their diet closely reflected the available seed types. Cereal grain spilt at harvest, and other stale seeds were the main food in the non-breeding season. It was proposed that this low-quality food limited breeding. When milk-ripe grass seeds and cereal grains became available, mice switched their diet to these fresh foods. Breeding started about a month later. The onset of breeding in different habitats was asynchronous. These findings suggest that time of onset of breeding was determined by available food supplies.

The hypothesis that breeding of mice in rice fields in spring is limited by food supplies which are inadequate in energy or quality was tested in a field experiment. Three types of supplemental food were provided *ad libitum* to mice in a rice field in spring 1981. The breeding performance of the mice was monitored by capture-mark-release censusing. After six weeks,

banks with supplementary food supported a significantly higher proportion of breeding mice than control banks. There was no evidence of an effect on the breeding performance due to the different food qualities, and hence the energy content of the diet was probably the main factor limiting breeding.

The hypothesis that breeding in rice fields in autumn and early winter is limited by poor food quality was also tested. At that time, mice on the farm ate a diet of nearly pure rice, and caged mice fed pure rice produced few or no litters. Supplements of casein or germinated rice grain significantly improved both litter production and litter size, but supplements of vitamin, gibberellic acid (GA_3), mealworms or milk-ripe rice grain did not. It was concluded that protein was probably the limiting nutrient for breeding of mice eating rice diets.

A field experiment with a 2^2 factorial design was conducted in a rice stubble field in autumn 1983. It had been suggested in previous studies that high population densities might also lead to suppression of breeding by house mice. Therefore, population density was also included as a treatment in this field experiment. The treatments were supplementary High-protein Food or Low-protein Food, and Culled or Unculled mouse numbers. Supplementary feeding increased the protein content of the diet from 8% to 11%, and was associated with a significant increase in the proportion of pregnant and lactating females on grids. Neither the culling treatment, nor the interaction of culling x food-quality had a significant effect on the proportion of breeding females.

The results of the experiments indicate that onset of breeding in spring was limited by food availability, with an energy shortage probaby the main factor, and that breeding in autumn was limited by food quality, with inadequate protein probably the main factor.

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CHAPTER ONE

INTRODUCTION

1.1. FOOD AND OTHER FACTORS AFFECTING REPRODUCTION OF SMALL MAMMALS

This study investigates the hypothesis that the breeding of the house mouse *Mus musculus* on cereal farms in the Murrumbidgee Irrigation Region (MIR) is limited by food. House mice are capable of breeding all year round, but field populations usually cease breeding in winter and, even during the breeding season, do not realize their full reproductive potential. This sub-maximal productivity is usually attributed to the food supplies being inadequate in either energy content or quality, with social inhibition and low temperatures often being suggested as contributory factors (DeLong 1967; Newsome 1969a,b, and 1970; Newsome and Corbett 1975; Bronson 1979; Pryor and Bronson 1981; Redhead 1982; King 1982). Experimental data to support this hypothesis are lacking for two main reasons. First, it is difficult to assess the nutritional status of wild mice or the supply and quality of food in their environment. Further, in natural populations, several factors probably act in concert to regulate reproduction, and so the role played by food may be obscured or modified by other environmental, social or genetic factors.

Many field studies of small rodents have found a correlation between changes in the food supply, diet or nutritional status of individuals, and changes in reproductive parameters such as the percentage of adult females pregnant or lactating in a population, the average litter size, or the duration of the breeding season (Jameson 1953 *Peromyscus maniculatus* and *P. boylei*; Smith 1954, *Mus musculus*; Hoffmann 1958, *Microtus californicus*; Adamczewska 1961, *Apodemus flavicollis*; Zejda 1962, *Clethrionomys*

glareolus; Newson 1963, *Clethrionomys glareolus*; Smyth 1966, *Apodemus sylvaticus* and *Clethrionomys glareolus*; Beatley 1969 and 1976, *Dipodomys merriami*, *D. deserti*, *D. microps*, *Perognathus longimembris* and *P. formosus*; Newsome, 1969a, *Mus musculus*; Batzli and Pitelka 1971, *Microtus californicus*; Bradley and Mauer 1971, *Dipodomys merriami*; Hansson 1971, *Apodemus sylvaticus* and *Clethrionomys glareolus*; Field 1975, *Lemniscomys striatus* and *Praomys natalensis*; Newsome and Corbett 1975, *Mus musculus*, *Notomys alexis* and *Rattus villosissimus*; Taylor and Green 1976, *Arvicanthis niloticus*, *Mastomys natalensis* and *Rhabdomys pumilia*; Cengal *et al.* 1978, *Microtus pinetorium*; Cole and Batzli 1979, *Microtus ochrogaster*; Getz *et al.* 1979, *Microtus ochrogaster*; Lam 1980 and 1983, *Rattus argentiventer*; Breed 1981, *Notomys alexis*; King 1982, *Mus musculus*; Redhead 1982, *Mus musculus*; Batzli and Pitelka 1983, *Lemmus sibiricus*; Gibson and Delany 1984, *Clethrionomys glareolus* and *Apodemus sylvaticus*; Lindroth and Batzli 1984, *Microtus pennsylvanicus*). The results of these studies are often interpreted as evidence for a causal relationship between food supply and reproduction. Stronger evidence for such causal relationships comes from experimental studies in which reproductive parameters are compared for populations whose only major difference is the nutritional resources available. This is usually accomplished by setting up experimental plots in a fairly uniform environment, providing supplementary food on some plots, and comparing the reproductive performance of the populations on plots with the extra food to that of populations on the control plots. The results of 20 such studies on rodents are presented in Table 1.1. The main problem in the interpretation of many of the studies is a lack of treatment replication. Without replicates, the natural variability between sites cannot be measured, and hence it is not possible to determine whether observed differences in breeding performance between experimental and control sites are due to a treatment effect or are merely a location effect (Hayne 1978; Hurlbert 1984). A second problem with the

studies, is that not all give consistent results, even when the same species were studied. Often, the authors suggest that other environmental or social factors had an effect on breeding performance, especially in those studies where a food effect on breeding was not recorded. Despite these problems, it is clear that reproduction in many small rodent species is food limited, as in fifteen of the studies, and ten species, the supply of supplementary food affected one or more aspects of breeding performance. Unfortunately, although food supply was found to affect breeding performance, it was often unclear whether it was available energy, or particular nutrients that were limiting. Only Negus and Berger (1977) and Cole and Batzli (1978) specified that it was quality of the food rather than its energy content that was important.

Food supply has the potential to limit breeding either through a shortage of energy, or through an undersupply or imbalance of particular nutrients or chemical factors that are needed for reproduction. Relatively little is known about the effects of dietary protein restriction, restricted food intake, or starvation on plasma gonadotrophins in the mouse (Rattner *et al.* 1979), but there have been many investigations of these effects in the rat (Callard and Leathem 1970; Howland 1971; Saitoh and Takahashi 1977; Campbell *et al.* 1977; Lintern-Moore and Everitt 1978). Leathem (1961, 1966 and 1970) found dietary deficiencies in rats and mice prevents the normal development and functioning of the reproductive organs. Other authors have shown that ovarian failure in rats fed protein deficient diets can be prevented by the injection of luteotrophic or gonadotrophic hormones, and concluded that these diets cause reduced activity of the endocrine glands which comprise the hypophyseal-gonadal axis (Nelson and Evans 1955; Guinnina and Leathem 1974). Such findings led Leathem to describe rodents that are fed inadequate diets as 'functionally hypophysectomized', but additional mechanisms are

also involved. Fielden and Brumby (1962) restricted the food intake of hypophysectomized albino mice, and found fewer ovulated compared to controls fed *ad libitum*, and in those that did ovulate, produced fewer ova were produced. They concluded that reduced food intake alters the ovarian response through mechanisms other than those involving the pituitary gland. Lamond and Bindon (1969) found that restricting the food of albino mice, followed by *ad libitum* feeding caused an unusually large number of ova to be released, and suggested that this might be because FSH stores in the pituitary gland are raised during the period of food restriction, and these large stores are released once *ad libitum* feeding is resumed. Hastings and Zeman (1979) found that both food restriction and protein deficiency led to reduced levels of serum triiodothyronine and free (unbound) thyroxine in pregnant rats. Hypothyroidism reduces appetite, interferes with body protein storage, and inhibits the conversion of carotene to vitamin A (Leathem 1961). Hence deficiencies in one nutrient may lead to an endocrine imbalance which leads to further deficiencies, which may prevent the needs of reproduction being met.

It has been proposed that first oestrous in rats may not occur until a critical body weight or body fat content is attained, and hence that the energy content of the diet may determine the age at which rats reach puberty (Kennedy and Mitra 1963; Frisch *et al.* 1977). Studies on laboratory mice do not support this hypothesis. As examples, Hansen *et al.* (1983) found mice with a restricted food intake had a lower body weight and a lower body fat content at puberty, than control mice with a high food intake. Vandenbergh *et al.* (1972) found that mice on a high protein diet had accelerated sexual development, but this was not accompanied by accelerated body growth. Thus while both the energy content and the protein content of the diet can affect the age at which puberty is attained, the authors of both studies concluded that this is not because the diet affects the age at

which a critical body weight or body fat content is attained.

There is a lack of information available about the minimum requirements of nutrients needed for successful reproduction by house mice. While information and recipes for stock diets that have nutrient levels adequate to support breeding in populations of caged mice are readily available (Bruce and Parkes 1949 and 1956; Hoag and Dickie 1960; Ford 1977; National Research Council 1978; Ralston Purina Company 1978; Knapka 1983), these probably supply many nutrients far in excess of minimum requirements, and in excess of levels supplied by most natural diets of wild mice.

The main energy demands for reproduction come during late gestation and throughout lactation. For small rodents which produce large litters, the supply of energy at these times may be critical. At birth a house mouse litter is about a quarter the weight of the mother, but is about 1.5 times the mother's weight after only two weeks suckling (Widdowson 1981). Some comparative measurements of house mouse food consumption for non-breeding, pregnant and lactating females obtained from studies on caged mice are presented in Table 1.2, and these show that food consumption may increase to 3 to 4 times non-pregnant levels during lactation. Reproductively active males may also use extra energy patrolling their territories, and in fighting and chasing.

Studies on caged mice have shown that they usually have their first litter at the age of six to eight weeks, and thereafter breed about every four weeks, and the number of young produced per litter is most commonly six to eight (Pelikan 1981; Berry 1981b; Sage 1981; Wallace 1981). Even small restrictions in energy intake can prevent successful fertilization and implantation in house mice. Albino females given no food for thirty hours, at or about the time of mating, have reduced litter production (McClure 1967a,b). The main factors are failure of

ovulation and death of ova before implantation. The fasting causes hypoglycaemia, and McClure suggests that this inhibits adeno-hypophysial function. Rattner *et al.* (1978a) found a 48 h fast between days two and four of gestation in albino mice suppresses the plasma concentration of luteinizing hormone and progesterone and abolishes surges of prolactin. Small restrictions in food intake during early pregnancy causes increased failure of implantation (Rattner *et al.* 1978b and 1979). They found moderate (35%) and severe (65%) reduction of *ad libitum* consumption decreases the weight of the ovaries and uterus, and may interrupt implantation and terminate pregnancy. Male albino mice given no food for 36 to 48 hours have a reduced libido for two days after the end of the fast (McClure 1966). Pairs of inbred house mice given restricted food for 18 days before mating, show increased barrenness, mainly due to a failure of many pairs to copulate (Truscott *et al.* 1974; Wodzicka-Tomaszewska *et al.* 1974). A correlation between food consumption per mouse and fecundity has been found for wild-strain house mice kept in large groups in pens (Southwick 1955).

Even if energy requirements for reproduction are met, undersupplies of particular nutrients can also impair reproductive performance. Studies with caged house mice (mainly laboratory strains), have shown that deficiencies of particular vitamins, minerals, essential fatty acids, or protein can impair reproductive performance. Chemical factors such as phytohormones, secondary plant compounds, or toxins have been suggested also as having possible stimulatory or inhibitory effects on breeding (Section 2.4). Howie and Porter 1950; Deol and Truslove 1957; Hoag and Dickie 1960; National Research Council 1978; Olsen 1981; Ward 1981; Pryor and Bronson 1981; Sakanari 1983). In addition, laboratory strains of house mice and rats (*Rattus norvegicus*), fed nutrient-deficient diets, often develop anorexia, and so suffer from an energy deficiency (Russel 1948; Kwong and Barnes

1977).

Diets deficient in energy or nutrients have been shown to have the following effects on the reproductive performance of caged house mice: delayed sexual maturity and a lower body weight at puberty for young females (Vandenbergh *et al.* 1972; Hansen *et al.* 1983); irregularity, lengthening or complete prevention of oestrous cycling in adult females; plus an increased incidence of failure to copulate and increased barrenness, or a reduced frequency of litter production, a decrease in litter size and weight, a decrease in milk production, an increase in cannibalism, and a reduced weaning success (White and Andervont 1943; White and White 1944; Ball *et al.* 1947; Carr *et al.* 1949; Lee *et al.* 1952; Visscher *et al.* 1952; Truscott *et al.* 1974; Smart and Silence 1977; Zamiri 1978; Heasley 1983). A protein deficient diet fed to male house mice prevents maturation of the testes and impairs spermatogenesis (Leathem and DeFeo 1952; Leathem 1970). These effects have also been demonstrated for laboratory rats fed inadequate diets (Nelson and Evans 1953; Brown *et al.* 1960; Chow and Lee 1964; Richardson *et al.* 1964; Widdowson and Cowen 1972; Barnes *et al.* 1973; Saitoh and Takahashi 1975; Frisch *et al.* 1977; Mokhtar *et al.* 1977; Walker and Bethia 1977; Hasting-Roberts and Zeman 1979; Merry and Holehan 1979; Galler *et al.* 1980; Pond and Wu 1981).

The enviromental factors that affect breeding in natural populations of house mice have been reviewed by Bronson (1979). He suggests that there are relatively few non-social environmental factors that routinely affect breeding of natural populations. In addition to 1) the energy content and 2) nutrient quality of the food supply discussed above, he thinks only 3) 'diurnal modulation by daily light:dark cycles' and 4) temperature are important. Out of points 1) and 2), he clearly thinks that energy intake is more important than nutrition: 'The broad

range of diets acceptable to this species suggests that seasonal variation in specific nutrients might not be a normal cause for seasonal breeding . . . There can be no doubt that if seasonal variation in energy intake occurs, seasonal breeding will also occur.' Regarding point 3), he considers that light:dark cycles are important only in fine-tuning the timing of events of the oestrous cycle, and thinks that 'the available evidence certainly suggests that photoperiodic regulation of reproduction in house mice is either quite weak, or more probably, is totally absent', and therefore that seasonal changes in photoperiod will not influence birth rates. A later study by Pryor and Bronsen (1981) on wild-strain mice kept under two strictly controlled photoperiod regimes supports this conclusion. This means that house mice are not obligate seasonal breeders. Regarding point 4), Bronson considers that temperature does have an important effect on reproduction, and this factor is briefly reviewed below.

Experiments on caged mice have shown that temperatures of 5°C or below cause increases in nestling mortality and delays in vaginal opening in young females; and in adult females cause increased barrenness, longer oestrus cycles and reduced litter size and frequency (Biggers *et al.* 1958; Pennycuik 1972a,b and 1973; Pryor and Bronson 1981). High temperatures, over 28°C, also suppress reproduction (Biggers *et al.* 1958; Pennycuik 1969). House mice, however, are well able to adapt to temperature extremes. When caged mice are exposed to low temperatures they modify the ambient temperature they are exposed to by burrowing, nest-building and huddling in groups (Prychodko 1958; Barnett 1965; Wolfe and Barnett 1977; Pennycuik 1974). Crowcroft and Rowe (1957) found mice kept in pens bred well if they had adequate food, even when temperatures were below freezing for long periods, and Laurie (1946) found they can breed well at temperatures as low as -10°C. Barnett and his co-workers have shown that mice moved from a warm environment (21 or 23°C) to a cold

one (-3 or 3°C), had fewer fecund pairs than those that stayed in the warm environments. But mice kept in the cold showed both genetic and ontogenetic selection for increased fecundity, and after eight generations, the mean young weaned per pair in cold environments matched that of pairs kept in the warm (Barnett 1973; Barnett *et al.* 1975). Maternal effects were particularly important for adaptation to breeding in the cold (Barnett 1973; Barnett and Dickson 1984a). For example, when wild-strain mice were kept at -3°C for ten generations, the milk of lactating females was higher in fat content (a genetic adaptation), and the offspring had a higher milk intake (an ontogenetic adaptation), and were heavier at ten days of age, than those of controls kept at 23°C (Barnett and Dickson 1984b). The ability of mice to adapt to low environmental temperatures led Bronson (1979) to suggest that in wild house mice 'seasonality of breeding in response to seasonal changes in temperature seems to carry a low probability'. However Pryor and Bronson's (1981) later work with caged mice, shows that the suppressive effect of low temperature on reproduction is more severe if conditions are also wet and variable. Hence in the wild, where winter conditions tend to be wet and uncertain, suppression of reproduction in house mice may be greater than that observed in the dry and steady cold environment imposed on mice in most laboratory tests.

Pryor and Bronson (1981) also found that for caged wild-strain mice the suppressive effects on reproduction imposed by cold temperature and poor-quality diet were additive. Mice appear to be able to breed well at low temperatures if they have a good food supply, and they also breed well on a sub-optimal food supply if temperatures are warm, but not if low temperatures and poor food supplies are combined. Other factors may also have an influential role. For example, Pennycuik (1974) suggested that the increased social contact that results from huddling behaviour at moderate to low temperatures (4°C or 21°C), may

induce social suppression of breeding even when food requirements are met. Breeding may also be associated with an increased intolerance and unwillingness to share nests (Brown 1953), which may result in reduced huddle size. This may lead to increased food requirements, as Prychodko (1958) found that house mice (an inbred strain) kept in groups of five had a food consumption 30% less than singly kept mice. Strecker (1955) found that when ambient temperatures were below freezing, food intake decreased, presumably because the mice stayed huddled in their warm nests, or possibly because they had entered torpor, which reduces oxygen consumption to one quarter non-torpid levels and so conserves energy (Morton 1978; Hudson and Scott 1979).

An environmental factor that may regulate breeding that is not listed by Bronson, but is proposed by Newsome (1970) is soil moisture. He believes mice are unable to burrow well in dry soils, and hence that dry soils may limit the availability of nest sites. This factor would only be likely to operate in arid environments and has been shown by Redhead (1982) not to be of significance on farms in the MIR in places where irrigation water keeps the soils moist. Therefore the seasonal pattern of breeding observed in most populations of wild house mice are likely to be due to the first three of Bronson's factors.

Theories on the social regulation of breeding in house mice are mainly based on observations of caged or enclosed populations of house mice. In high-density populations sexual maturity can be retarded or suppressed by either pheromonal cueing, or by activation of a stress mechanism (Christian and Davis 1964; Vandenbergh 1971; Bronson 1979; Drickamer 1981; Ramaley 1981). When a population is enclosed, the only females that breed are usually those present in the initial colony. Sometimes the females of first generation offspring will also breed but other females do not usually become reproductively mature (Rowe *et al.*

1964; DeLong 1978; and Van Zegeren 1980). Thus, as population density increases, the proportion of breeding females in the population declines (Strecker and Emlen 1953; Southwick 1958; Petrusewicz 1963; Barnett 1964; Lloyd and Christian 1969; Lloyd 1975). Eventually all females cease to breed (Christian 1956; Crowcroft and Rowe 1957; Lidicker 1965 and 1976; Stueck and Barrett 1978), and the population density stabilizes or slowly declines. Although most of the above studies were conducted on caged or enclosed mice, Bronson (1979) considers that 'The evidence from natural populations is conflicting but often supports the concept that some aspect of a high-density environment can interfere with reproductive performance'. The actual density at which breeding is suppressed is dependent on the complexity of the environment and it is probably the rate of social interaction rather than the actual density *per se* that is important (DeLong 1967; Stueck and Barrett 1978; Butler 1980; Berry 1981a). Vandenbergh *et al.* (1972) compared the effects of social factors and dietary protein levels on the regulation of sexual maturation in female laboratory mice. While both factors had significant effects, social factors accounted for 47.3% and dietary factors 4.8% of the total variance.

The extent to which social factors operate in wild populations has been little studied. Some Australian mouse populations, occassionally breed up to extremely high densities, and these irregular, temporary increases are called outbreaks or plagues. The occurrence of these plagues appears to be evidence against the social regulation of beeding in these natural populations. Anderson (1961), however, suggests that extremely favourable conditions may permit population explosions by causing the breakdown of the social mechanisms that usually regulate population density in house mice. An example of how this may operate is suggested by Redhead (1982) who thought that a high-quality food supply may weaken social suppression of breeding, and so

allow an increase in breeding intensity, and an extension of the breeding season of mice in the MIR. These hypotheses provide possible explanations for proposed links between unusually good food supplies and such outbreaks or plagues in Australian populations. Finlayson (1939) suggests that an increase or rejuvenation of vegetation leading to increased reproduction of house mice causes such outbreaks. Naumov (1972) also suggests that an abundant food supply on the Ukrainian steppes leads to increased reproduction and increases in population density similar to the Australian outbreaks. Bronson (1979) and Pryor and Bronson (1981) suggest that such outbreaks occur when climatic conditions yeild a food supply that provides maximum support for reproduction over an extended peiod of time. Newsome (1969a,b and 1970) thinks that if moist soils suitable for burrowing are available concurrently with abundant food, mice in the Australian wheat belt can 'multipty' sufficiently to cause a plague. These plagues or outbreaks do not appear to be the cyclic phenomena often reported for microtines and other small mammal species in the northern hemisphere (Elton 1942; Krebs and Myers 1974) but rather, irregular events that are ultimately linked to weather conditions (Newsome and Corbett 1975; Saunders and Giles 1977)

Reports of outbreaks come mainly from Australia (Newsome and Crowcroft 1971; Plomley 1972; Hone 1980; Redhead 1980; Williams and Wilson 1980; Chapman 1981), but also from California (Pearson 1963) and Chile (Fuentes and Campusano 1985). Estimates of the densities of mice in such plagues are rare, but Hall (1927) cited by Brown (1953) estimated densities at the centre of one plague in California at almost 170,000 mice per hectare, and Newsome and Crowcroft (1971) counted 297 active mouse burrow entrances in 0.44 ha of sheep pasture during a plague in South Australia. DeLong (1967), Newsome (1970) and Redhead (1982) all found that house mice build up to plague-like densities when abundant food is supplied on experimental sites. The main cause was immigra-

tion, but increased reproduction contributed in the first two studies. DeLong (1967) recorded a higher proportion of lactating females house mice on plots with extra food, and breeding also continued longer than that of controls. These effects did not continue indefinitely, however, and breeding ceased after the population density on the plots with the extra food had increased to high levels. Newsome found some mice remained in 'breeding condition' on his feeding plot throughout the fourteen month duration of his experiment. Unfortunately the population density on Newsome's control plot fell to nearly zero and he had no replicate sites, so it was not possible to conclude with certainty whether the prolonged breeding was due to his feeding treatment or to a location effect (Hurlbert 1984). Also Newsome's use of 'breeding condition' to measure reproduction, which presumably meant the proportion of adult females with perforate vaginae, rather than the proportion that were pregnant or lactating, does not indicate whether the mice on his plot were actually producing litters. Redhead recorded no breeding response to extra food. All three authors considered that breeding in field populations was regulated by social factors as well as by food supply.

Although DeLong (1967) showed that breeding in wild house mice may be limited by food supply, the question of whether it is an undersupply of energy or an undersupply of particular nutrients that limits breeding, has not been investigated prior to the present study. Pryor and Bronson (1981) believe that 'evidence for the overriding importance of the quality of the diet for reproduction in [house] mice seems substantial', but also consider that 'It is unclear at this time whether the reproductively important aspects of diet is caloric or nutritional'. Although food quality has been experimentally shown to affect the breeding of other species in the field, this has not been demonstrated for house mice. As the effect of food supplies on breeding has been proposed as an important factor in plague formation,

further understanding of this relationship is fundamental to further understanding the causes of such plagues. The the object of the present study, therefore, is to determine whether the breeding of mice in a habitat where plagues have occurred in the past, is limited by either food energy or nutritional quality.

1.2. AIMS OF THE PRESENT STUDY

There were four main aims:

i). *To describe the food supply, diet and breeding seasons of house mice on cereal farms in the MIR.*

This was to generate hypotheses about the effects food supply and diet have on reproductive performance.

The diet study required the development of a new method for the identification and quantification of the diet of house mice. Previous methods used for the analysis of house mouse diet were not considered sufficiently accurate. Data collected on diet and breeding seasons from January 1979 to April 1980 is described in Chapter Two.

The results of this initial part of the study led to the formulation of two hypotheses on the relationship between diet and reproduction. Their testing constituted the following aims.

ii). *To test the hypothesis that the breeding of house mice in rice fields in spring is limited by the food supplies which are inadequate in 1) energy content, or 2) nutritional quality.*

The data collected in the first section of this study (Chapter Two) showed that the onset of post-winter breeding was asyn-

chronous in different crops, but was synchronous with the times that seeds ripened and were eaten, and it was suggested this was a causal relationship. A field experiment was conducted from September to November 1981 to test this hypothesis. This is described in Chapter Three.

iii). *To test the hypothesis that a diet of pure rice is of inadequate nutritional quality to support reproduction in house mice, and if so, to determine which nutrients are lacking in a rice diet.*

In Chapter Two it is suggested that the poor quality of the food eaten by mice in stubble fields limits breeding. Laboratory experiments were conducted on the effects of food quality using caged mice kept under controlled conditions. These experiments were conducted when field work was not in progress and are described in Chapter Four.

iv). *To test the hypothesis that breeding of house mice in rice fields in autumn is limited by poor food quality.*

Data presented in Chapter Two show that when mice in the rice stubble fields were on a diet of nearly pure rice grain breeding declined and eventually stopped. Data presented in Chapter Four show that a pure rice diet is nutritionally inadequate to support breeding. This led to the development of the hypothesis that the decline of breeding in rice stubble fields is caused by the poor-quality diet. This was in line with the hypothesis developed by Redhead (1982), that the autumn decline in breeding in rice stubble fields is caused by low-quality food interacting with high population density to suppress breeding. His model, though untested, was based on a large body of empirical data. With this background, it seemed advisable to investigate the effects of both food quality and population density

together. A field experiment to test the limitation of breeding by these two factors was conducted from March to June 1983, and it is described in Chapter Five.

1.3. STUDY SITES AND STUDY ANIMALS

All study sites were cereal farms within 30 km of the town of Griffith (34°18'S, 146°04'E in the Murrumbidgee Irrigation Region (MIR), where Redhead's (1982) demographic study of house mice was conducted. Information from Redhead's study about mice in this region was of help in the planning of experimental details in the present study, such as the location, frequency and intensity of trapping, and the amount of food to put out and the number of replicate treatments to conduct. By the time the first field experiment was being planned in the present study (January 1981), some information was available from his study on population turnover rates, normal timing and duration of breeding, home range or territory size, and fluctuations in population density. By the time the second field experiment was being planned (June 1982), he had developed a model to describe and explain changes in population density, stucture and breeding.

During the present study, mouse numbers in the MIR fluctuated. Redhead found that it is usual for there to be moderate to high densities of mice in this region, with annual cycles of abundance. Numbers increase through summer and autumn, while breeding is in progress, and then decline through winter and spring. In 1979 numbers were high, and in early 1980 there was a local outbreak in the study area. An unforseen disappearance of mice then occurred from July to November 1980, and until May 1981 very few mice were caught. Numbers then increased again and resumed their usual annual fluctuations for the remainder of the study period.

The irrigated cereal farms used as study sites were all intensively cultivated for cereal production with fat lamb raising as a side line. The principal crop grown on these farms is rice (*Oryza sativa*), which is also the largest income earner, but other crops are grown in rotation. All crops are grown in irrigated bays separated by low contour banks which follow the slope of the land at 7.5 cm intervals. These contour banks are about 1.0 m wide and 0.5 m high (Figure 1.1) with shallow ditches along their edges. They often support a dense weed growth. The bays range in size from 0.5 to 7 ha, depending on the slope of the land. The irrigation water is brought to the fields in open channels (Figure 1.2), whose banks also usually have a dense weed growth.

Rice is sown in late September or early October, and on the farms used in the present study it was combine sown: the seed bed is ploughed and the seeds are placed in drills, at a depth of less than 2.5 cm. After sowing the bays are flush irrigated by intermittent flooding at intervals of about ten to fifteen days, which is frequent enough to prevent the soil from drying out. When the rice is about 20 cm tall, permanent water is held in the bays, at a depth of at least 5 cm, (Figure 1.3) and this remains for about 100 days, being drained about two weeks before harvest. Harvest usually occurs from mid-March to mid-April. The maximum area of rice allowed per farm is 80 ha but not all farmers grow this amount. Other crops include winter crops of wheat (*Triticum aestivum*) and two-row-barley (*Hordeum distichon*), which are sown about June and usually harvested in late November, and summer crops of sorghum (*Sorghum bicolor*), corn (*Zea mays*) and sunflower (*Helianthus annuus*) which have similar sowing and harvesting times to rice. Two rice crops are often grown in the same field in successive years. Alternatively, a winter crop may be sown into a rice stubble field. If stubble fields are not used for a

crop, lambs are usually put out to graze, and clover (*Trifolium* spp.) may be sown to improve the pasture.

The weeds on these cereal farms are mainly exotic herb and grass species which are common world-wide on agricultural land. The irrigation of fields promotes the growth of these weeds, and the grasses grow rapidly and seed early, often up to six weeks earlier than the cereal crops they germinate with. Such grass seeds provide an early and abundant food source for the mice living in these fields.

Active predators on the study sites included black-shouldered kites (*Elanus notatus*), black-backed magpies (*Gymnorhina tibicen*), barn owls (*Tyto alba*), Australian ravens (*Corvus coronoides*), foxes (*Vulpes vulpes*), feral cats (*Felis domesticus*) and brown snakes (*Pseudonaja textilis*). Black rats (*Rattus rattus*) were also occassionally present, though in such low numbers that it seems unlikely they would have affected the mouse populations.

Weather data for the present study was obtained from the CSIRO meteorological station in Griffith. Annual rainfall varies widely, but the mean total is 404 mm. On average the rainfall is evenly distributed between all months of the year, but there are wide variations about the monthly means. Mean monthly temperatures range from the hottest month of January (mean min. 16.2°C, mean max. 31.8°C) to the coldest month of July (mean min. 2.8°C, mean max. 14.1°C). Weekly mean maximum and minimum temperatures and total rainfalls are given in the relevant chapters for each period when field studies were conducted.

All mice used in the present study were wild strain house mice from the MIR. The present taxonomic status of the Australian house mouse is still uncertain (Redhead 1982), but the field

of house mouse taxonomy is presently in a state of review (Berry 1981b; Marshall 1981; Marshall and Sage 1981; Sage 1981). Other studies on house mice which are referred to in this thesis include both wild strain, which come from commensal or field populations, or are randomly bred decendants of these types, and laboratory mice, which include all strains of domesticated *Mus musculus* which have had their genetic development controlled by man. The terms 'mouse' and 'mice' are used in this thesis only for house mice, and all other species are given their generic names.

Table 1.1. Results of previous experiments with supplementary feeding of unenclosed rodent populations.

Effects of feeding treatment:

A. Increased proportion of females that breed*.
B. Increased frequency of litter production.
C. Increased average litter size.
D. Increased length of breeding* season.
E. Increased juvenile survival.
F. Earlier sexual maturity.
G. Increased female numbers.
H. Increased total numbers.

Species	Number of experiment sites**	Number of control sites**	Food type supplied	Duration of feeding	Effect of supplementary feeding A	B	C	D	E	F	G	H	Reference
Mus musculus	2	3	crimped oats and chick starter mash	14 months	yes	–	–	yes	no	–	yes	yes	DeLong (1967)
Mus musculus	1	1	wheat grain	14 months	?	–	–	yes	–	–	yes	yes	Newsome (1970)
Mus musculus	2	2	wheat grain	3 months	no	no	no	–	–	–	yes	yes	Redhead (1982)
Apodemus sylvaticus	1	1	oats or wheat grain	2 years	yes	–	–	yes	–	–	–	–	Watts (1970)
Apodemus sylvaticus	1	1	wheat grain	21 months	–	–	–	?	yes	–	–	yes	Flowerdew (1972)

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Table 1.1. continued.

Species	Number of experiment sites**	Number of control sites**	Food type supplied	Duration of feeding	Effect of supplementary feeding A	B	C	D	E	F	G	H	Reference
Apodemus sylvaticus	1	1	wheat grain	21 months	yes	–	–	?	–	–	–	–	Flowerdew (1973)
Clethrionomys glareolus	1	1	oats or wheat grain	2 years	yes	–	–	yes	–	–	–	–	Watts (1970)
Clethrionomys glareolus	1	1	wheat grain	21 months	no	–	–	no	–	–	–	–	Flowerdew (1973)
Clethrionomys glareolus	2	2	oats	2 years	yes	–	–	yes	no		yes	yes	Andrzjewski (1975)
Clethrionomys rutilus	2	1	oats and sunflower seed	3 winters	–	–	–	no	?	no	yes	yes	Gilbert and Krebs (1981)
Peromyscus leucopus	1	2	wheat grain	1 year	?	no	no	no	yes	?	yes	yes	Bendell (1959)
Peromyscus leucopus	1	1	Purina mouse chow	15 months	?	–	–	yes	yes	yes	yes	yes	Hansen and Batzli (1978)
Peromyscus polionotus	1	1	bird seed	3 years	–	–	–	–	–	–	–	yes	Smith (1971)

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Table 1.1. continued.

Species	Number of experiment sites**	Number of control sites**	Food type supplied	Duration of feeding	Effect of supplementary feeding A	B	C	D	E	F	G	H	Reference
Peromyscus maniculatus	3	3	whole oats	7 months	yes	–	–	yes	no	–	yes	yes	Fordham (1971)
Peromyscus maniculatus	3	1	oats	18 months	yes	–	–	yes	?	yes	yes	yes	Taitt (1981)
Peromyscus maniculatus	2	1	oats and sunflower seeds	3 winters	–	–	–	no	?	no	yes	yes	Gilbert and Krebs (1981)
Microtus montanus	3	3	green wheatgrass	2 weeks	yes	–	–	yes	–	–	–	–	Negus and Berger (1977)
Microtus californicus	1	1	oats, corn and chick starter mash	13 months	no	–	–	no	no	–	no	no	Krebs and DeLong (1965)
Microtus californicus	3	4	carrots, barley and corn	8 months	yes	–	–	yes	–	–	–	yes	Ford and Pitelka (1984)
Microtus ochrogaster	1	1	rabbit pellets	about 18 months	yes	–	yes	no	?	–	–	yes	Cole and Batzli (1978)

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Table 1.1 continued

Species	Number of experiment sites**	Number of control sites**	Food type supplied	Duration of feeding	Effect of supplementary feeding A	B	C	D	E	F	G	H	Reference
Microtus townsendii	1	2	lab chow and oats	4 months	–	–	–	no	–	–	no	no	Taitt *et al.* (1981)
Microtus townsendii	1	2	whole oats	4 months	no	–	–	yes	no	–	yes	yes	Taitt and Krebs (1981)
Microtus townsendii	1	1	whole oats	3 months	yes	–	–	yes	–	–	yes	yes	Taitt and Krebs (1983)
Mastomys natalensis	1	1	wheat grain	12 months	no	–	–	no	–	–	yes	yes	Taylor and Green (1976)
Arvicanthis niloticus	1	1	wheat grain	12 months	yes	–	–	yes	–	–	no	yes	Taylor and Green (1976)

* Breeding refers to animals actually pregnant or lactating, not just in 'breeding condition'.
** Where there are no replicate experimental and control sites, the results may only indicate a location effect rather than a treatment effect (Hurlbert 1984).
Question marks indicate a suggested effect only.

Table 1.2. Food consumption of breeding and non-breeding house mice.

Reproductive condition	Sex	Grams food per mouse per day	Type of food	Mean body weight g	Mouse strain	Ambient temperature °C	reference
Not pregnant or lactating	both	2.8	pearl barley	14.6	wild	–	Newsome (1967)
Not pregnant or lactating	both	3.2	pellets	20	inbred	21 to 23	Wood and Nishimura (1968)
Not pregnant or lactating	both	4.6	sheep nuts	20	wild	20 to 25	Winterbourn (1973)
Not pregnant or lactating	"	3.9	dog biscuits	"	"	"	" "
Not pregnant or lactating	female	2.8	formula diet at 13.6% protein	13	Swiss	–	Goettsch (1960)
Gestation (first 18 days)	"	4.0	"	–	"	–	" "
Lactation (first 17 days)	"	7.6	"	–	"	–	" "
Virgin	female	4.6	–	22	white	21	Barnett and Little (1965)
Lactation (first 10 days)	"	9.0	–	22	"	"	" " "

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Table 1.2 (cont.)

Reproductive condition	Sex	Grams food per mouse per day	Type of food	Mean body weight g	Mouse strain	Ambient temperature °C	reference
Gestation (day 1)	female	3.8	pellets with 4.2 Kcal/gram	21	white	–	Myrcha *et al.* (1969)
Gestation (next 19 days)	"	5.1	"	21 to 29	"	–	" " "
Lactation (first 26 days)	"	8.0	"	28	"	–	" " "
Gestation (days 5 and 6)	female	2.4	purina lab chow	27	white	–	Heasley (1983)
Gestation (days 12 to 19)	"	6.0	" " "	33 to 46	"	–	" "
Lactation (first 10 days)	"	8.4	" " "	33	"	–	" "

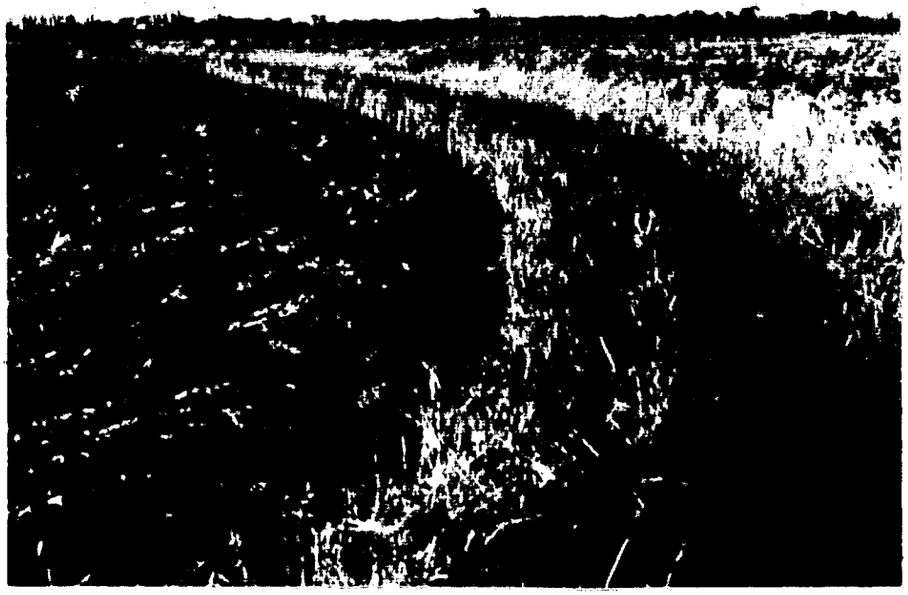


Figure 1.1. Contour bank in ripe rice crop. Barnyard grass and other weeds provide food and shelter for mice.

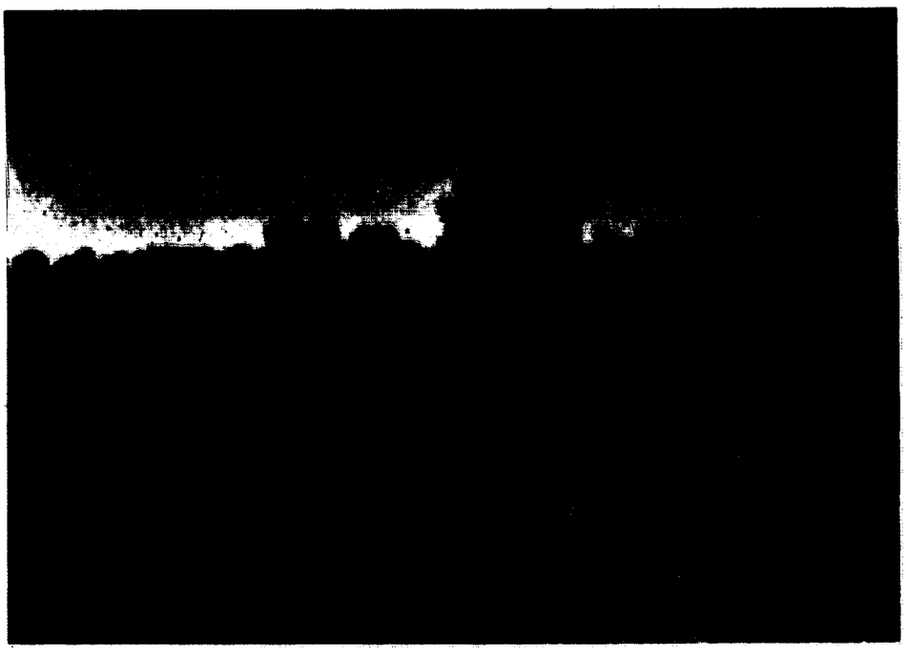


Figure 1.2. Channels distribute irrigation water throughout the farms. Their banks have an abundant weed cover and provide a year-round habitat for mice.



Figure 1.3. Flooded rice bays. When the rice crop is flooded (October to February), the contour banks provide a favourable habitat for mice. Plant species on the foreground bank include Patersons curse, spear thistle and wild oats, and the seeds of all three species were found in the stomachs of mice caught in this habitat.

CHAPTER TWO

FOOD SUPPLY, DIET AND BREEDING SEASONS

2.1. INTRODUCTION

Information on variations in the diet, and in the timing and intensity of breeding of house mice, was required so that hypotheses could be formulated on the role of food supply as a factor affecting reproduction. Some information was available from previous studies.

Seventeen studies were found in which the natural diet of house mice is described: nine for cultivated habitats, and eight for uncultivated habitats (Table 2.1). These studies show that the main foods are seeds and insects, with smaller quantities of other invertebrates and leaf, root and stem tissue. Less frequent items are fruit, fungus, feathers, grit and vertebrate flesh. The variation in the relative amounts of plant and animal tissue recorded in different studies, apparently reflects the availability of foods in the different habitats, but it is probably also partly due to the different techniques used to analyse the diets, as discussed later in this section.

Seeds were the main food in all the studies conducted in cultivated habitats. In the studies conducted in uncultivated habitats, animal tissue was the main food in three, seeds were the main food in three, and in two both plant and animal foods were recorded but the relative amounts are not given. There are obvious seasonal changes in the proportions of plant and animal food found in many of these studies, but no pattern common to most of them can be discerned. While some sub-species of wild house mice apparently hoard food (Naumov 1940, *Mus musculus*

hortulanus; Hamar 1960, *M. m. spicilegus* Hamajima 1962, *M. m. molossinus*), this is apparently only to meet their maintenance requirements over winter when food is scarce, and is not used as a reserve to meet breeding requirements.

There have been many studies on the duration of the breeding seasons of free-living house mice, both for commensal populations (in buildings, grain stores, haystacks and ricks, food stores, and bird enclosures), and for wild populations (on both cultivated and uncultivated land). In commensal populations, where food supplies are relatively constant, breeding is usual throughout the year, often with little change in intensity (Laurie 1946; Smith 1954; Rowe and Swinney 1977; Anderson 1978; Pelikan 1981; Rowe *et al.* 1983; Singleton 1983). In contrast, wild mice usually cease breeding for at least four months in winter (Naumov 1940; Breakey 1963; Pearson 1963; Lidicker 1966; Batten and Berry 1967; Berry 1968; Newsome 1969a,b; Thomson 1979; Myers 1974; Morton 1978; Stickel 1979; Smiet *et al.* 1980; Williams and Wilson 1980; Chapman 1981; Gleeson 1981; Pelikan 1981). Only four records were found of winter breeding in wild mice, and this corresponded with unusually abundant winter food, either from supplementary feeding (DeLong 1967; Newsome 1970), or from an exceptionally abundant or prolonged natural seed yield (King 1982; Redhead 1982).

The question of whether it is an undersupply of energy or an undersupply of particular nutrients, that limits breeding of house mice in the field, has not been investigated prior to the present study. To fully understand the pathways through which natural diets affect reproduction, information is required on 1) availability and consumption rates of preferred foods, 2) chemical composition of natural diets, 3) nutritional physiology, 4) digestibility of foods, and 5) nutrient and energy requirements for reproduction. With such information a model can be constuc-

ted matching intake of nutrients and energy against requirements for breeding, to see if quantities are adequate. The main problem with this approach is the difficulty in collecting data of sufficient accuracy to make a meaningful model. Information on some of these five points is available for some house mouse populations, but no comprehensive study of all five points has been attempted for any population. Even if the resources were available for such a study, however, it is doubtful if such information would be of use in determining if breeding is limited by food, as variations of just 2 - 4% in intake of dietary nutrients may determine whether breeding will be food limited (Bruce and Parkes 1949; Lee *et al.* 1952; Hoag and Dickie 1962; Knapka 1983). Presently available methods for collecting data on points 1 and 2 are far from capable of achieving this degree of accuracy. For example, in a study on rabbit nutrient requirements for reproduction by Myers and Bults (1977), the protein content of the food and the stomach contents was measured separately by chemical analyses, and the protein content of the stomach contents were found to exceed that of the food by between 0% and 53% for different foods, making the use of correction factors of dubious accuracy necessary when estimates of the nutrient composition of unknown foods were to be made from stomach content analyses. Similar levels of error were probably introduced in the study by Sadlier *et al.* (1973) in which food consumption rates of *Peromyscus maniculatus* in the field were estimated from data for faecal production rates. The errors involved in the identification and quantification of the food types in natural diets from stomach analysis are discussed later in this section. In any event, assessing an animal's nutrient requirements for breeding, and then showing that their consumption of these nutrients in the field does not meet these requirements, as attempted by Sadlier *et al.* (op. cit.) for the protein and energy requirements for reproduction in P. maniculatus, will not prove that breeding is limited by these nutrients. Presumably if ani-

mals are prevented from breeding by some factor other than food, such as social suppression or lack of nest sites, they are not going to consume nutrients at the high level required for reproduction.

In the present study, rather than attempting to collect data on all five of the above points, so that a complete model could be constructed of nutrient supply and demand pathways, the more traditional approach was followed of attempting to demonstrate food limitation of breeding by experimentally manipulating food supplies in the field, and monitoring the breeding response. Such an approach still required data on points 1, 2 and 5, so that hypotheses could be formulated regarding when nutrients or energy might be limiting and which nutrients might be involved, but it did not require the precise and accurate data needed for a descriptive model of nutrient or energy pathways. Therefore the first step of the present study was to collect this type of descriptive data for mice in the field, the second step was to use this data basis formulate such hypotheses, and the final step was to test these hypotheses by field experimentation.

To understand the role of food supply as a possible limiting factor in house mouse reproduction, it is necessary to separate the effects of food supply from other factors that may also be influencial. The factors that are likely to affect the breeding of mice in the MIR are discussed earlier (Section 1.1) where it is suggested that while social regulation of breeding in field populations is still poorly understood, it seems likely that the only environmental factors of importance are 1) caloric intake, 2) nutrition, and 3) temperature. Bronson (1979) thinks it is difficult to determine which environmental factors act to limit breeding in the field: 'Where one finds the most obvious correlation between environmental factors and reproduction in the wild - namely, in seasonal breeding, one also finds virtually no capa-

city to separate and examine individually the various ambient factors which could provide a causal variation'. This applies in most temperate environments because food supply and temperature usually change together: warm spring temperatures are associated with increased plant growth and hence food supply, and cooler autumn temperatures are associated with the end of seed production and a decline in food supply. To assess the role of food supplies independently of temperature, experimental areas with the same temperature conditions but contrasting food conditions are needed. On rice farms in the MIR rotational cropping is practised, and crops at different stages of maturity grow in neighbouring fields. Consequently mice living in neighbouring fields are exposed to equal temperatures and daylengths, but to contrasting conditions of food supply and food quality. If food regulates breeding, mice living in different crops would be expected to have breeding seasons out of phase with each other but in phase with the growing seasons of the crops they are feeding on. If, on the other hand, temperature regulates breeding, then mice would be expected to have their breeding intensity correlated with changes in temperature and the breeding seasons of mice living in different crops would be in phase with each other.

To determine whether variations in breeding intensity or duration were associated with changes in diet, the different foods eaten by mice had to be identified and quantified, to show seasonal and habitat variations in diet. A new method of diet analysis was developed for this purpose, because the methods of diet analysis described in previous studies on house mouse diet were not considered suitable as discussed briefly below.

Faecal analyses (Watts 1970a; Watts and Braithwaite 1978; Thompson 1979; Cockburn 1980) have a serious drawback; they tend to overestimate items that are resistant to digestion, such as

plant vascular tissue and insect cuticle, and underestimate or even omit items that are quickly digested, such as endosperm tissue and soft thin-cuticled leaves. The identification of material in faecal samples is also often difficult. These problems have been discussed in detail by Hannson (1970) and Neal *et al.* (1974).

Descriptions of diet based on analyses of stomach contents are more likely to give reliable quantitative data. The accuracy of identification depends on the magnification used for examination, and the reliability of the reference material. Sakhno (1957), Houtcooper (1978), Thompson (1979) and Gleeson (1981) spread the contents of each stomach in a dish and examined them under a stereo microscope at low magnification, to identify the food types present, and estimate their relative volumes. They only separated diet items into general categories, such as seed, vegetative plant tissue, and animal tissue, and did not identify the types of seed eaten unless they had a particularly distinctive appearance. Berry (1968) and Berry and Tricker (1969) also separated the foods into these general categories, but did not describe the methods they used. When foods of similar appearance, such as chewed up seeds from different plants, are mixed together in a stomach, and their separate identification and quantification are required, the above methods are inadequate. Only Naumov (1940) and Whitaker (1966) believed that they identified many food items in the stomachs of house mice to genus or species level, but neither described the methods used. Identification of seeds to species level usually requires the preparation of microscope slides and analysis under a high-powered compound microscope (Hansson 1970). A technique, suitable for this purpose, and for the volume and composition of material found in house mouse stomachs, was developed in the present study, and is described in Section 2.2.5.

In this chapter the results of eighteen months data collection on the diet and breeding seasons of mice in different crop habitats on irrigated cereal farms are described. In addition, seasonal changes in food availability and body fat levels are recorded for mice in rice fields. Correlations between diet and breeding season are discussed, and possible cause and effect relationships are hypothesized.

2.2. METHODS

2.2.1. Study site

This study was conducted on two neighbouring farms (Farms 25D and 25H in the Benerembah district, 20 km southwest of Griffith, NSW (34°17'S., 146°2'E.) in the MIR. Temperature and rainfall data for the study period are presented in Figure 2.1.

Two winter crops were grown on the study farms; wheat (60 ha) and two-row barley (50 ha). These were sown in June, reached the milk-ripe stage in October, and were harvested in November. Three summer crops were grown: rice of the variety inga, a long grain type (160 ha), sorghum (45 ha), and sunflower (30 ha). Rice crops were grown on both farms and were sown in late September and early October, and harvested in late March. The sunflower and sorghum crops were sown in late October and not harvested until May and June respectively. Irrigation water was applied to the wheat, barley, sorghum and sunflower crops in a series of intermittent flushes. Water would temporarily flood the bays between the contour banks, and then would be drained away, and further irrigation water would be applied before the soil dried out. The rice crop was initially irrigated with intermittent flushes, but from late October to early February it

was flooded with permanent irrigation water. After harvest, the stubble was left fallow. The barley and wheat stubble was used as sheep pasture and the wheat stubble was aerially sown with clover seed in early April.

2.2.2. Collection of mice

Mice were required for stomachs and for determination of breeding seasons. Trapping was conducted from January 1979 to April 1980 in six habitats: wheat field, barley field, rice contour banks, rice stubble, sorghum field, and channel banks. The trap-sessions were conducted at intervals of about one month. In each trap-session, the aim was to collect from each habitat, at least ten adult females, and a sample of ten stomachs, each with a volume of at least 0.3 ml. When mouse densities were low, or when the sex ratio was biased in favour of males, sample sizes were smaller. Mice were caught in break-back traps (Supreme brand). The traps were baited with a small piece of leather soaked with linseed oil. The advantage of this bait was that it was not swallowed and so did not contaminate the stomach contents. Longworth traps were tested for collecting mice for dietary analysis, but were unsuitable because of the rapid rate of passage of food through the mouse's gut. Even when Longworth traps were checked at hourly intervals, the stomachs of mice caught in them usually contained insufficient material for analysis.

Traps were laid out in lines of fifty, with single traps placed at 8 m intervals. In wheat, barley and sorghum fields, trap-lines were run through the crops or stubble. In rice this was not possible owing to the permanent flooding of the crops, so until harvest, trap-lines were set only along contour banks. After the rice harvest, trapping on contour banks continued, but

trap-lines were also set in the stubble. In the channel-bank habitat, traps were set along the top or sides of the banks. Captured mice were taken from traps at dawn to prevent predation by Australian ravens (*Corvus coronoides*), black rats (*Rattus rattus*) or other mice. The stomachs were immediately removed and their volume was determined by measuring the amount of water displaced when they were dipped into a graduated glass tube. Only stomachs with a volume of at least 0.3 ml contained enough food material for analysis; other stomachs were rejected. A small nick was made in the side of each stomach with the point of a scalpel blade, and the stomachs were then stored singly in vials containing a 70% ethanol solution. The uteri of adult females were checked macroscopically for the presence of embryos, and the numbers in the right and left horns recorded. The presence of any undersized embryos was also noted, but these were rare, and were not included in the embryo counts.

Between 100 and 200 traps were set in each habitat on trap nights. Trapping continued for four nights, or fewer if enough mice were caught sooner. Traps were moved to a new location each night, as the success rate of traps left in one location for more than one night was usually low. Trap-lines were also placed in new locations in successive monthly trap-sessions to avoid over-trapping the population in particular areas.

The number of mice caught per one hundred trap-nights was taken as an index of numbers. One trap-night was one trap set for one night. Estimates of population densities could not be made from this type of kill trapping data.

2.2.3. Available seed types

In each trap-session, a search was made in each habitat for

specimens of all plant species present. Samples were collected, pressed, and identification was made mainly by reference to Cunningham *et al.* (1982). Lists were made of all species found and the presence of unripe seeds, ripe seeds or fruits was recorded. In addition, the soil surface was examined for fallen seeds. Probably only common seed types were found by this method. The lists, however, gave an indication of the diversity of seeds available, and provided a guide for identifying seeds present in stomach contents.

Except for rice grain, no quantitative measurements were made of seed availability, but each seed type found was recorded as present or abundant. Seeds classified as abundant were found throughout a habitat in such large quantities that all mice must have been able to find enough of them to more than meet their dietary requirements.

2.2.4. Seed foods

All seeds identified in the stomachs of wild-caught mice were classified as 'known' seed foods. Seed types which were found in the trap-habitats, but which were never identified in the stomachs of wild-caught mice, were classified as either 'likely' or 'unlikely' seed foods on the basis of the following test. Each seed type was collected in sufficient quantities to feed a mouse for several days. If a wild-caught mouse offered a seed type *ad libitum* for 48 h, ate it readily, remained active after the 48 h, and had at least 0.2 ml of the seed material in its stomach on autopsy at the end of the test, the seed was described as a likely seed food. If these three conditions were not met, the seed was offered to a second, and then a third mouse. If either the second or third mouse met the three conditions, the seed was still classified as a likely seed food. If

none of the mice met the three conditions the seed was classified as an unlikely seed food.

2.2.5. Diet analysis

This section describes the development of the method used for the identification and quantification of foods present in the stomachs of mice. There were three steps involved:

i) Preparation of slides.
ii) Identification of food.
iii) Quantification of food.

In each of these steps, the objective was to develop a method that was both time-efficient and accurate. This sometimes involved comparing alternative techniques and selecting the one most suitable.

i) *Preparation of slides.* Each stomach was removed from the 70% ethanol solution and the contents were tipped into a petri dish and thoroughly mixed to a homogenous paste by chopping the mixture with a curved scalpel blade. This chopping broke up any large fragments, or lumps of compacted material, and mixed together the separate layers of material present in some stomachs.

Two microscope slides were prepared from the contents of each stomach. One 'untreated' slide was prepared from a sample of stomach material taken straight from the petri dish after mixing (Figure 2.2a,b,c,d,e). A second 'acid-treated' slide was made from a sample cleaned by incubating about 0.2 ml of stomach material in a solution of nitric (7%) and chromic (10%) acids at 80°C for ten minutes, following Fitzgerald (1976), but using only half her acid concentrations. This treatment dissolved away all starch and most other amorphous endosperm and cotyledon material, and left cleaned pieces of seed coat. These were a valuable aid

to identification (Figure 2.3a,b).

For the preparation of both untreated and acid-treated slides, a drop of melted glycerine jelly (Bancroft 1967), was stirred thoroughly into about 0.05 ml of stomach material on a slide to ensure a random distribution of particles. A 22 X 50 mm cover slip was pressed down firmly to remove air bubbles. When the glycerine jelly set, a coating of nail varnish was applied to the edges of the cover-slip to seal it. Staining was unnecessary because all slides were observed under polarised light, which heightened colour contrasts between food fragments, and created bi-refringence crosses in starch granules.

ii) *Identification of food.* Initial observations on the stomach contents of mice caught on rice farms showed that seeds comprised about 90% of most stomach contents. Effort was concentrated therefore, on developing a technique to identify the main seed types found in the stomachs of wild-caught mice, preferably to species level. Other foods were classified only as invertebrate (arthropod and annelid) or as vegetative (leaf, stem, root, bud and fruit tissue). Separating stomach material into invertebrate, vegetative and seed categories on the basis of their microscopic appearance was straightforward, as these foods have distinctive appearances. As the non-seed foods formed only a small part of the diet, investment of time in further classifying such items was not thought worthwhile.

An initial investigation was undertaken to meet the following two objectives: 1) to determine which parts of the digestive tract contained material which could be readily identified under the microscope, 2) to determine the best material to be used in the preparation of reference slides to be used as an aid in the identification of unknown material obtained from the digestive tracts of wild caught mice.

Five seeds were chosen as representative seed types, namely rice, wheat, sunflower, alfalfa and phalaris. These seeds were fed to mice for five days with only one seed type given to each mouse. The mice were then killed, and samples were taken from the stomach, small intestine, caecum and rectum. Samples of these five seeds were also obtained by removing any husk or seed coat material that could readily be cracked and peeled by hand, and grinding a small sample of each seed in a Wiley mill to particle sizes similar to those found in samples taken from mouse intestines. One untreated and one acid-treated slide were prepared from each gut and ground seed sample, as described above. Slides were observed at 40x and 100x magnification under polarized light.

Virtually all stomach material was identifiable and there were distinct differences in the appearance of the food material taken from the stomachs of mice that had eaten different seeds. In contrast, slides prepared from samples taken from further down the alimentary canal had a much greater proportion of unidentifiable material, because the distinctive starch granules were mostly digested and many distinctive structural features of the seed coats were destroyed. At least half the material in slides prepared from rectal material was unidentifiable. So it was concluded that the identification of unknown seeds eaten by wild house mice would be best achieved by the analysis of stomach contents only.

The material in slides prepared from stomach contents bore little resemblance to the material in slides prepared from the same type of seeds which had been ground in a Wiley mill. In the slides of stomach material, the starch granules were more fragmentated, and there was much less seed coat material than in the slides of milled seeds. These differences were so great that

milling was rejected as a method for preparing reference material.

Therefore, in the preparation of reference slides, material taken from the stomachs of mice which had been fed a pure seed diet for forty-eight hours was always used. All seed types found in the habitats monitored in the diet study are listed with their generic names in Table 2.2. Each of these seed types was offered to a caged mouse to eat. If the first mouse did not eat the seed, it was offered to two others. If none of the mice ate the seed, it was not included in the reference collection. When a seed type was eaten by a mouse, it was fed *ad libitum* on this seed for forty-eight hours, and was given no other food. Its stomach contents were then used to prepare an untreated and an acid-treated reference slide. Reference slides were also prepared by this method for some fungi, tuberous root and fern spores; but these plant materials were not observed in slides prepared from the stomach contents of wild-caught mice.

Identification of all seeds in the stomach samples taken from wild mice was based on comparisons with the reference slides. Dicotyledon seeds were mainly identified on the basis of seed coat structure, observed at 100x magnification on acid-treated slides. Seed coats varied in the number and appearance of the layers present, colour, surface markings, presence and type of hairs, cell size and shape, and cell wall thickness. Such variations are quite characteristic for most seeds and furnish a means of positive identification, at least to genus level (Foster and Gifford 1974; Esau 1977). But the extent to which mice ingested dicotyledon seed coat fragments varied, being dependent largely on seed size. The seed coats of small seeds, such as peppercress (Figure 2.2a) and nightshade, were usually chewed and swallowed, but very small seeds, such as tufted bluebell, were usually swallowed whole. Mice tended to be more

efficient at husking medium-sized seeds, such as docks (Figure 2.2b) and medics, but usually ate a sufficient amount of seed coat fragments to make identification possible. When eating large dicotyledon seeds, with a hard seed coat which could be easily cracked open and removed, such as Bathurst burr, variegated thistle or paddy melon seeds, mice usually discarded all the seed coat material, and ate mainly cotyledon tissue. This last group of dicotyledon seeds was the most difficult to identify, and they were usually classified as 'unknown dicotyledon seeds'

For monocotyledon seeds, seed coats in acid-treated slides were an aid to identification, but the starch granules in the slides of untreated stomach material often furnished the quickest means of reliably identifying them (Figure 2.2,d,e). The size, shape and aggregation pattern of starch granules in both cereal grains and grass seeds were usually distinctive. Schoch and Maywald (1967) stated that most common starch granules 'are readily and unequivocally identifiable under the microscope'. Exceptions in this study were a few monocotyledon seeds, such as those of rice and barnyard grass, which had very small, fragmented starch granules (Figure 2.2c). The examination of seed-coat structure on acid-treated slides often helped in the identification of these types of seed (Figure 2.3,b), but even so, some seeds did not have distinctive structural characteristics in their seed coats, and so could not be identified to species level.

A list of seeds available in each trapping habitat was made each month, and this helped with identification by narrowing down the number of choices available. Occasional seed fragments were found in the stomachs of wild-caught mice for which there was no corresponding reference slide, and they could not be identified. Unidentified seeds were classified only as monocotyledon or di-

cotyledon, and if dicotyledon, they were further classified as being either starchy or non-starchy.

iii) *Quantification of food.* The aim was to quantify the proportions by volume of food types in the stomach contents of house mice. Traditional methods rely mainly on counts of the relative frequency of particles (Sparks and Malechek 1968; Hansson 1970; Reichman 1975; Cockburn 1981; Fulk *et al.* 1981), or on measurements of the areas covered by fragments (Williams 1962 and 1969; Gebczynska and Myrcha 1966; Watts 1968; Wheeler 1970; Neal *et al.* 1974; Cengal *et al.* 1978). These methods were developed mainly for the analysis of herbivore diets, and their reliability is usually dependent on the accuracy of the assumption that the surface area of identifiable food fragments is a known function of the relative volume or weight of these foods. While this may hold true for leaf-eaters, if the thickness of leaf particles is relatively constant, there are no grounds for accepting it for the foods eaten by house mice. Material from their stomachs was finely masticated, and particle dimensions varied from approximately spherical starch granules, as small as 1 µm in diameter, to thin flat strips of plant epidermis, up to 2 mm in diameter. Lumps of endosperm and invertebrate tissue were irregularly shaped and varied in thickness. The large variations in the dimensions of particles meant that data collected by either of the above methods would not have accurately reflected the relative volume of the diet items in the stomach samples (Hansson 1970). Many stomachs were found to contain large numbers of very small particles of less than 5 µm which would have made the use of such methods extremely time consuming and inaccurate, and on starchy samples virtually impossible. These problems could have been partly overcome by screening the stomach samples through a mesh to unify particle size (Williams 1962; Watts 1968; Hansson 1970; Wheeler 1970; Reichman 1975; Thomson 1979; Cockburn 1981). But this approach was rejected because

screening would have caused a very biased loss of diet components, and the greatest relative loss would have been starchy endosperm, the mice's main food.

The method developed in this study used subjective estimates of the relative volumes of food types present in slides of untreated stomach content material. Series of test-slides were prepared from mixtures of measured volumes taken from the stomach contents of caged mice fed a single food for forty-eight hours before death. Stomach samples of pure rice, barley and alfalfa seeds, and green wheat plant were collected from ten mice for each food. Caged mice would not eat sufficient quantities of any of the insect types offered, for an adequate sample to be collected, so a simulated insect stomach sample was prepared. Flour beetles (*Tribolium* spp.) were mixed with a small quantity of 70% ethanol and ground with a mortar and pestle until the resultant paste had a particle size and consistency similar to samples taken from mouse stomachs.

Test-slides were made from untreated mixtures of these food samples with proportions by volume of each food type ranging from 2.5% to 97.5% of the total volume. These test-slides were used for practice at making estimates of relative volumes, until accuracy was developed. On each slide twenty non-overlapping, systematically spaced fields-of-view were examined under 40x magnification. In each field of view, the total food volume was considered to be 100% and the percentage volume contributed by each food type was estimated and given a value ranging from 0% to 100%. The mean of the twenty values recorded for a particular food type was taken as the estimated percentage volume of that food type in the stomach. Hansson (1970) found that twenty fields-of-view is sufficient for an accurate assessment of relative volumes in the analysis of diet slides. In the present study, it was found that the estimates of the mean percentage

volume of the main food types changed little if extra fields-of-view were observed. Ten fields-of-view would have been sufficient for reasonably accurate estimates of the volume of major food types, but twenty fields-of-view gave better estimates of the relative volumes of the minor food types. After a test-slide had been visually scored, the estimated percentage volumes of the food types were compared to the true values. More than 100 test-slides were used for practice to develop skill at making accurate estimates.

The accuracy of the method was then tested on four series of untreated test-slides in which percentage volume of food types ranged from 0% to 100%. After the test-slides were prepared, their identification numbers were covered with stickers and they were randomly mixed. The percentage volumes of the food types in each slide were estimated, and the stickers were removed only after the whole series of slides had been scored. For each test-slide series, the estimated mean percentage volume of each food type for each slide (y) was regressed on the actual percentage volume for that slide (x) to give a regression line ($y = a + bx$) for each series. If the estimates were perfect, the regression equation would have given $y = x$, so the closeness of the intercept 'a', and the regression coefficient 'b', to 0.0 and 1.0 respectively, gives an indication of bias (accuracy of the method). The percentage of variance accounted for by the regression equation was also calculated, and this gave a measure of the random errors associated with the estimates (precision of the method).

Three series of test-slides of two-food mixtures were examined, and one series of a three-food mixture. Data plots, regression lines and values for the percentage of variance accounted for by the regression for the data sets for the three two-food mixtures are presented in Figure 2.4a,b,c, and for the single three-food mixture in Figure 2.5a,b,c. The lines of best

fit through the data were all close to y = x, and the percentage of variance accounted for by the regression equations was above 93% for all the two-food mixtures. In the three-food mixture, the regression line for the estimated percentages of the two main foods accounted for more than 91% of the total variance, but for beetle, the food type present in the smallest quantities, the regression line accounted for only 76.7%. Even so, the maximum deviation from the true value in these beetle estimates was only 10%. It was concluded that the levels of error and bias in the four data sets obtained from these series of test-slides were all within acceptable limits for the purposes of the present study.

Of the 501 stomachs from wild-caught mice eventually analysed, 487 (97%) had three or fewer food types making up at least 90% of the stomach contents by volume. Therefore a method which gave accurate estimates for a mixture of three foods is considered adequate for the present study.

The above method was used for quantification when a stomach contained food fragments that could be separately identified by the method described above. When seed types of similar appearance were mixed in a stomach, only the combined percentage volume of these mixtures was usually estimated. An exception was made when rice grain and barnyard grass seeds were together. The starch grains of these seeds were indistinguishable in untreated slides, but the seed-coat fragments observed in acid-treated slides were distinctive and easily identified (Figure 2.3a,b). The relative volumes of these two seeds in a stomach were determined from the relative areas of seed coat observed in acid-treated slides. To determine the relationship between seed-coat area and seed volume, ten caged mice were fed diets of pure rice or pure barnyard grass for 48 h. The contents of their stomachs were collected and eight acid-treated test-slides were prepared from mixtures containing 50% rice stomach content and 50% barn-

yard grass stomach content by volume. These were observed at 100x magnification through an eyepiece with an insert engraved with a grid pattern which gave a background of 100 squares to each field-of-view. The number of squares covered by rice seed coat fragments (r), and barnyard seed coat fragments (b), were counted in twenty fields-of-view. The percentage rice seed coat ($r\% = 100\Sigma r/(\Sigma r + \Sigma b)$ was then calculated for the eight slides. The mean r% for the eight slides was 50.5±3.4 (one standard error). This was so close to 50% that the r% calculated for cleared slides prepared from the stomach content of mice with mixtures of these two seeds in their stomachs was taken as a direct estimate of the proportion of rice by volume in the mixture. (For example, a stomach which contained 60% rice/barnyard mixture, and 40% other food, with an r% value of 25%, would be scored as 15% rice, 45% barnyard grass, and 40% other foods.)

The number of stomachs (N) which must be analysed to obtain a reliable estimate of the relative volume of foods eaten by animals in a population depends largely on the variability of the diet. Hanson and Graybill (1956) give a formula for calculating the number of stomachs needed for calculating the mean volume of a particular food item with 95% confidence limits: $N = 4\sigma^2/e^2$ where 'σ' is the standard deviation of the estimated volumes of that food, and 'e' is the allowable error, which can be set at any level acceptable to the experimenter. When the population being sampled has a varied diet and 'e' is set at 5% or less, 'N' is often in excess of 100 stomachs (Watts 1968). Sample sizes in the present study were usually much smaller than those required to give an error as low as 5%. The mean sample size used in the present study was eight, but when trap-success was low, still smaller samples were used. Large sample sizes were not feasible because of the trapping effort required, the disturbance to the population that would have resulted from the removal of many mice, and the time involved for analysis. Hence, in seasons

and habitats where the mice were eating a diverse diet, the standard errors of the mean percentage volumes of food types were large. Standard errors are therefore given for the mean volumes of the main foods eaten in the diet analysis results (Figure 2.7), as a guide to the degree of caution needed in the interpretation of these estimates. (The 95% confidence limits lie within two standard errors either side of the mean.) In habitats where one preferred food type was abundant and formed the diet staple, the standard errors are low, and hence a sample of about eight was adequate for an accurate estimation of food volumes. As examples, the rice-based diet eaten in the rice stubble habitat from March to June (Figure 2.7a) was accurately determined. In contrast, mice living on channel banks (Figure 2.7b), where many foods were available, were eating a diverse diet, and in samples taken from this habitat the standard errors are large. In such samples the data shown in the figures are best considered as indications only of the types and diversity of foods being eaten, not as reliable estimates of mean percentage volumes in the diet.

Analyses of variance tests were conducted on six randomly selected data sets to determine levels of within-slide and between-slide variance. One example, from the stomachs analysed from the barley crop habitat in September 1979, is presented in Table 2.3. Within-slide variance was far less than between-slide variance for more than 90% of foods in the six tests. This indicated that twenty fields-of-view was adequate to give a reasonable estimate of the mean percentage volume of foods in a stomach, and that most of the error in the quantitative estimates was due to the small sample sizes of stomachs collected. For the example given in Table 2.3, Hansen and Graybill's formula indicates that 158 stomachs would have been needed to achieve 95% confidence that the true mean per cent volume of the main food (barley grass seed) lay within 5% of the estimated mean. Al-

though small samples were sometimes used in the present study, and this led to wide confidence intervals around the volume estimates, they were still sufficiently accurate in most cases to pinpoint both the major and minor foods, and to clearly indicate seasonal changes in diet.

In summary, the above method has the potential to give accurate estimates of diet, with respect to both identification and quantification of foods, provided an adequate sample of stomachs are analysed. The method did not rely on any conversion factors relating particle frequencies or areas to volume. The assumptions made in previous studies about the validity in using such conversion factors for a species which eats such a diverse range of foods, seem doubtful. This new method is superior to other methods used to analyse the diet of house mice because foods that are similar in appearance can be separately identified and quantified, and because many seeds can be identified to species level, by the structure of their seed coats and the appearance of starch grains. Such accuracy was not possible in the methods of macroscopic analysis described previously for house mouse diet analysis.

The mean percentage volume of foods in stomachs is presented graphically (Figure 2.7a,b,c,d,e,f). This method of presentation is one frequently used for diet studies (Drozdz 1966; Watts 1968; Wheeler 1970; Batzli and Pitelka 1971; Cengal *et al.* 1978; Cole and Batzli 1979; Thomson 1979; Gleeson 1981), and it clearly shows the diversity and relative quantities of foods eaten. Therefore it is useful for making comparisons of diets between seasons and habitats. Its main drawback is that it can give a false impression of the accuracy of the estimates of mean volumes of food eaten, especially if these means have a large standard error.

2.2.6. Food supply in rice fields

Quantitative measurements of food abundance in rice fields were made by two methods. The initial method was developed by Newsome (1967) who measured food supplies in the field by confining mice in randomly placed bottomless bins which were hammered into the ground. Each bin covered an area of 0.11 m^2. The number of hours a mouse in a bin could maintain its body weight, by eating the natural food available, was used to estimate the amount of food available on that area of ground. Newsome used a regression equation which contained parameters for the initial body weight of the mouse (W), the time it maintained its weight (T), and the soil moisture content (M) to estimate the available food (F). He tested the accuracy of the method with mice placed in bins which had all the natural food removed and replaced with a measured quantity of food (pearl barley grain). His equation accounted for 73.8% of the observed variation. He assumed soil moisture affected soil surface temperatures, and so presumably had an effect on the metabolic rates of the mice, and hence their food energy requirements.

Soil moisture was not measured in the present study. Instead soil-surface temperatures were measured with maximum/minimum thermometers placed on the floor of each bin in a shaded position. There was little variation between bins in the temperature range recorded within sampling periods. The initial body weights of Newsome's mice ranged over 13.3 g, from 8.8 g to 22.1 g. In the present study the maximum range of initial body weights in any one sample was only 6.5 g (12.0 to 18.0 for 27 February; 9.7 to 16.2 for 30 March; 10.0 to 16.1 for 1 May; 11.2 to 17.7 for 20 July). Hence, variation in initial body weight and surface temperature within sampling periods was small in the present study. In field calibrations of the method using known quantities of food in bins, these two parameters were not found

to affect the time period body for which weights were maintained. Measured quantities of food were provided for mice in bin which had all the natural food removed, and regressions of 'T' on the known values of 'F' (T = aF) were conducted for each data set. In March the regression accounted for 96.1% of the observed variation in the data, in May for 93.7%, but in July for only 56.9% (Figure 2.6a,b,c). Therefore, the regression lines for March and May were used confidently to estimate 'F' values from measured 'T' values, but the July regression equation was used with less confidence.

This modification of Newsome's method was used to measure food supplies when average quantities of available food were in excess of 10 g/m^2 (February, March and May 1979). But when levels fell lower (in July 1979) 'T' values of zero were recorded, even though rice grain could still be found on the ground. The mice, which were present in high densities from June to August, were apparently finding sufficient rice for survival (Figure 2.7a). It was concluded that Newsome's method is not suitable for measuring a scarce food supply. As reliable measurements of scarce food supplies were required, an alternative method of quadrat sampling for rice grain was used. The analysis of the diet of mice in rice stubble in 1979 (Figure 2.7a), showed that rice grain constituted more than 90% of the diet for the first five months after the crop ripened, from late February to late July, and more than 70% for a further two months. This indicated that a measure of the available rice grain would give a good index of food availability.

Harvesting machines cut the rice heads from the stalks, strip off the grain, and drop the straw in rows. Some grain is left on the straw, so rows with straw dropped on them have far more rice grain than rows not covered by straw. For quadrat sampling, stubble fields were treated as two sub-habitats: rows

with or without straw. Sometimes narrow strips of rice were left unharvested, and these were treated as a third sub-habitat. A series of transects were run across the stubble fields in random locations to measure the areas covered by each sub-habitat. Then randomly located 0.25 m^2 quadrats were laid out in each sub-habitat. In each quadrat all straw, stubble, loose soil and grain was collected with the aid of secateurs, dustpan and broom. The rice grain was then sorted from the straw and soil by hand, oven dried at 80°C to constant weight, and weighed. The mean dry weight of grain in grams/m^2 was then calculated for each sub-habitat, and these figures were multiplied by the proportion of the field area covered by each sub-habitat and summed to give estimated dry weights of rice per square metre for the stubble habitat as a whole. This method measured food supply even when rice grain availability was less than 0.2 g/m^2.

2.2.7. Body Fat

The bodies of mice trapped for diet analysis in the present study were given to Redhead for body fat analysis, and he has presented the results elsewhere (Redhead 1982). Some bodies of mice trapped in rice fields, were analysed in the present study, using Redhead's methods. On collection from the traps, stomachs were removed and the bodies frozen. Each carcass was dried overnight in a vacuum oven at 60°C, pulverised in a blender for 15 seconds and placed in a pre-weighed, single thickness, 22 x 80 mm, cellulose thimble. Carcass plus thimble were weighed to obtain the total dry weight (DW) of the carcass. Fat was extracted for five hours with technical grade carbon tetrachloride in a Soxhlet apparatus. The thimbles and contents were re-dried overnight at 60°C, left to cool in a desiccator and then weighed to give the fat-free (lean) body weight (LDW). Total body fat (FAT)

was calculated as FAT = DW - LDW to give the proportion of fat (% FAT) as a percentage of dry weight, i.e.

$$\% \text{ FAT} = 100 \text{ (FAT/DW)}$$

A preliminary analysis, in which two batches of five carcasses were subjected to two consecutive extractions, each of five hours, showed that all removable fat had been extracted in the first five hours.

2.2.8. Protein content of seeds

Seed samples were dried at 90°C, ground to pass through a 1 mm mesh, and analysed for nitrogen content by semi-micro Kjeldahl digestion (Williams and Twine 1967). Nitrogen content was converted to percent protein content using the conversion factors in tables of protein contents (Food and Agricultural Organization 1970).

2.3. RESULTS

2.3.1. Available seed types

The 'known' and 'likely' seed foods found in all the habitats where trapping was conducted are listed by month and habitat in Table 2.4a,b,c,d,e. Each seed type is classified as either present or abundant (Section 2.2.3).

Seeds were scarce in all the habitats in late winter and early spring, when the only available seeds were those left from the previous season, and small quantities of ungerminated grain from previous crops or from sowing.

The winter irrigation of wheat and barley fields promoted a dense growth of grasses. The first of these grasses to ripen was barley grass which had milk-ripe seeds in early September (Figure 2.8). (Milk-ripe seeds are full-sized or nearly so, with their endosperm filled out with starch granules, but they are still green and if squeezed, exude a 'milky' juice.) This was followed about three weeks later by ryegrass and phalaris, and by October the wheat and barley grain had reached the milk-ripe stage. There were few fresh dicotyledon seeds available during this period in these habitats.

Winter-growing grasses, such as barley grass and phalaris, were scarce in the rice fields, and were absent from the sorghum fields in spring, probably owing to the lack of winter irrigation and the application of herbicides in these fields. The few grass plants found on rice banks ripened later than those in winter-irrigated habitats, and milk-ripe grass seeds were not recorded on contour banks in rice fields until November. An abundant supply of fresh seeds was not available until seeds of spring growing barnyard grass ripened in January in the rice crop and February in the sorghum crop. In late February, rice and sorghum grain both reached the milk-ripe stage.

A wide variety of dicotyledon weeds seeded in most stubble fields, especially on the contour banks, and seeds of dock, medics and thistles were common. An exception was the sorghum stubble where there was little weed growth and where most of the species that did grow were classified as 'unlikely' seed foods. The wheat stubble was sown with clover for pasture and this provided an additional food.

On channel banks, a wide variety of 'known' and 'likely' seed foods was available from spring until late autumn. Nearly all the grass and weed seeds available in crop fields were pre-

sent on the channel banks, though often in smaller quantities. Grain was sometimes spilt on the farm tracks which ran alongside the channel banks, and this provided additional food.

2.3.2. Diet

All 'known', 'likely' and 'unlikely' seed foods are listed in Table 2.2. A wide variety of seeds were acceptable food for mice. The diets of mice in the six trap-habitats monitored are presented in Figure 2.7a,b,c,d,e,f. Although some samples were small, the analysis was adequate to pinpoint both the major and minor foods eaten in most months and habitats, and to show the seasonal changes in diet, which achieved the aim of this section of the study. Seeds were the main food in all habitats and seasons. The mice were opportunistic feeders, and their diet closely reflected the available food types in the habitats where they were caught. They quickly switched from one food to another as available foods changed with season or with farming practices.

In the wheat and barley fields in winter (Figures 2.7c,d), mice ate a variety of food. In the barley crop this was mainly rice grain left on the ground from the previous rice crop, and blackberry nightshade seeds and fruit. Smaller quantities of other weed seeds and green plant tissue were also eaten. In the wheat field, wheat grain, presumably left ungerminated from sowing, together with stale weed seeds, such as fireweed and burr medic left from the previous autumn, made up the bulk of the diet in winter. But by August, green plant tissue was the main food, and this was mainly wheat plant tissue, especially the unemerged flower buds chewed out from the centre of the stems. Lepidopteran larvae and other invertebrates also made a significant contribution to the winter diet in wheat fields. Mice in the wheat and barley fields immediately switched their diet to spring

grasses when they reached the milk-ripe stage in September, and barley grass was the main food in both crops in this month. In October mice again switched their diet, this time to milk-ripe wheat or barley grain.

Monitoring the diet of mice on rice contour banks began in November, about a month after the crop was sown (Figure 2.7e). In November and December, rice grain made up about 60% of the diet. This grain was presumably left from sowing, or was left in the ground ungerminated from the previous year's crop. Spring grass seeds were the other main foods in these months. Mice switched their diet to barnyard grass as soon as it reached the milk-ripe stage in January, and then switched to milk-ripe rice grain when it became available about six weeks later. Monitoring of the diet of mice in sorghum began in February, when the mice in this habitat were eating large quantities of milk-ripe sorghum grain and smaller quantities of barnyard grass seed (Figure 2.7f).

As soon as cereal grains ripened, they were included in the diet, and constituted the major food in all habitats until several months after harvest. In the barley stubble, barley grain was still being recorded in the diet in August, some nine months after harvest (Figure 2.7d). In rice stubble, rice averaged more than 95% of the diet up until mid-July, four months after harvest, and was still 70% of the diet in late October, seven months after harvest (Figure 2.7a).

As grain supplies ran out in the stubble fields, mice switched to other foods. In wheat and barley stubble fields, dicotyledon weed seeds were the main substitutes. The main seeds eaten were curled dock, saffron thistle, wireweed, tufted bluebell, peppercress, and subterranean clover. Smaller quantities of burr medic, narrow-leaf dock, and unidentified seeds were also eaten.

In rice stubble, narrow-leaf dock and spear thistle were the main seeds eaten, and burr medic, curled dock, yellow wood sorrel and unidentified seeds were also recorded. In the sorghum stubble field where few weed seeds were available, and the main alternative food eaten after sorghum grain became scarce was earthworms, which were present in large numbers on the damp soil surface under piles of decomposing stubble.

On channel banks the diet was very varied, reflecting the wide range of food types available (Figure 2.7b). In spring, barley grass seeds were the first fresh seeds to be included in the diet, and these were followed by other grass seeds as they ripened: ryegrass, phalaris, wild oats, barnyard grass and others. A large number of different dicotyledon seeds were also eaten by the mice in this habitat. Those identified were curled dock, tufted bluebell, Paterson's curse, peppercress, burr medic and narrow-leaf dock. Many of the dicotyledon seeds eaten by mice in this habitat were not identified. The mice in this habitat also ate grain spilt on nearby farm tracks.

Invertebrate tissue was present in 39% of the stomachs examined. In the stomachs in which it was present it averaged only 9.4% of the stomach contents by volume. In most seasons and habitats it formed a small but consistent dietary supplement. Many of the invertebrates were clearly insects, including a large proportion of lepidopteran larvae. Earthworms were occasionally identified by the presence of chaetae. Vertebrate remains were found in stomachs only at times when chewed mice had been found in the traps, and this material consisted almost entirely of mouse hair and muscle. Such a food was considered unnatural; so stomachs containing this material were discarded.

Vegetable tissue was mostly leaf, stem, root and bud tissue. It was found in stomachs from all months and all habitats, being

present in 71% of stomachs. In stomachs where it was present, it constituted an average 7.7% of the stomach contents by volume.

Small amounts of grit were also found in many stomachs, especially when mice were feeding on spilt grain in stubble fields. This was probably accidentally ingested.

In summary, the different times irrigation water was applied to the fields determined the times when grass seeds and cereal grains became abundant in these fields. Hence the times these foods became the main foods eaten by mice varied between fields, from spring in the wheat and barley fields, summer in the rice fields, and autumn in the sorghum field. Once cereal grains ripened, they were the main food for several months is all fields, and only when these supplies were depleted did mice switch to other foods, including dicotyledon seeds and vegetable tissue.

2.3.3. Breeding

The data for the percentage of females pregnant in the habitats where trapping was conducted are presented in Figure 2.7a,b,c,d,e,f. The duration of the breeding season ranged from seven months in the barley crop, down to only three months in the sorghum crop. From June to September 1979, no breeding was recorded in any habitat. Breeding in different crops was asynchronous; breeding in winter crops and channel banks started and ended earlier than breeding in summer crops.

The best breeding performances were recorded in spring. For example, in the wheatfield in November, twelve adult females were caught, eleven of these were visibly pregnant, and the twelfth was lactating and had embryo scars. The mean litter size for

this sample was 8.5±0.5. The percentage of pregnant females peaked in wheat and barley fields in spring; in late summer on channel banks and rice contour banks and in rice stubble fields; and in autumn in the sorghum field. Breeding declined rapidly through summer in the wheat and barley fields, and no pregnancies were recorded in either of these habitats in autumn. In the rice and sorghum fields, breeding continued until the end of autumn.

The percentage of pregnant females in each habitat is plotted against mean minimum temperatures for the week preceding each trap-session in Figure 2.9. In the four months when no breeding was recorded in any habitat, the mean minimum temperatures were less than 8°C. In months when breeding was recorded, mean minimum temperatures were all above 8°C, but during these months there was no indication of any correlation between minimum temperatures and breeding intensity.

Mean litter sizes are presented in Figure 2.10 for all samples of three or more litters. A total of 108 litters were counted and the overall size mean was 7.30 ±0.20 (one S.E.). Sample sizes were only sufficiently large for analysis in the February, March and April catches in rice and sorghum fields. A two-way analysis of variance revealed that habitat had a significant effect on litter size ($F_{1,37} = 4.48$, $p<0.05$), but month did not ($F_{2,39} = 1.20$, $p>0.1$), and there was no significant interaction between these two factors ($F_{1,36} = 0.31$, $p>0.1$).

2.3.4. Numbers of mice

Seasonal changes in the numbers of mice caught per 100 trap-nights in the six habitats monitored are presented in Figure 2.11. In the wheat and barley fields, mouse numbers were high before breeding started, but declined when spring breeding began.

They remained low in these habitats through summer and autumn. In the rice crop, mouse numbers were moderate to low in the spring, but slowly built up once breeding began and increased through autumn to a winter peak. In the sorghum crop, there were few mice in summmer, but once breeding began they rapidly increased to peak in June, but then crashed in July.

2.3.5. Food supplies and body fat contents in rice fields

The measurements of food availability made by Newsome's method in 1979 are presented in Table 2.5. Abundant food became available on contour banks in late February, before the rice grain was ripe enough to provide a high-energy food source. Once the rice reached the milk-ripe stage in March, there was abundant food in the rice bays and this lasted until at least a month after harvest, but by late July rice grain supplies had fallen to levels too low to be recorded by Newsome's method.

The results of food availability measurements made by quadrat sampling are presented in Table 2.6, together with data for the body fats and numbers of mice at the time of sampling. Food supplies were measured in two rice stubble fields in June and August 1980, and then in June 1981, June 1982 and June 1983. In 1980 and 1981, the stubble fields sampled were those on the study site described above. The field on Farm J was used by Redhead (1982) as a study site also. Fields on other farms were used in later years.

Quadrat sampling revealed that about one tonne of grain per hectare was usually spilt on the ground at harvest. These supplies were rapidly depleted by foraging mice. Mouse numbers were high in 1980 and when grain was sampled on 18 June, supplies were already low. In the stubble field in Farm J, only 2.3 kg/ha were

available, about enough to feed 100 mice for a week. The number of mice per hectare in this field was probably much higher than this (Redhead pers. comm.), but numbers were declining. Redhead's (1982) population density index for the stubble field on farm J in April was 200, in June 60, in July 10, and in August was zero. By August the food supplies in this field were almost zero too, at only 1.6 kg/ha. The rice harvest on the neighbouring Farm B had been conducted about six weeks later than that of Farm J, and this was probably the main cause of food supplies on this farm being 9.3 times higher than those on Farm J in June. The body fats of mice on Farm B in June were also significantly higher than the Farm Jones ($F_{1,56} = 23.344$, $P<0.001$), which may have been due to the difference in available food. Mouse numbers were still high on Farm B at this time, but when sampling was conducted again in August, most of this food had gone and the mouse population had crashed, which is circumstancial evidence that the mice may have starved.

Quadrat sampling was conducted in the following winters to obtain information on the amount of variability in food availability between years. In June of 1981, food availability was nearly 500 times the 1980 value for Farm J. These abundant quantities were probably a result of the absence of foraging mice in this year, as the mouse population had not recovered from its 'crash' in the previous winter, and the trap-success was zero. In June 1982, sampling was conducted on two neighbouring rice fields on the farm study site described in Section 3.2.1. Food availability levels were intermediate between the 1980 and 1981 levels. In June 1983, the two rice crops monitored were the control grids on the study site described in Section 5.2.1. Harvest was unusually late this year, and rice grain was still abundant in June even though mouse numbers were high. In summary, there was a wide variation between years in available rice grain in stubble fields, and amounts were affected by both time

of harvest, and numbers of mice present.

In July 1979, twelve burrow systems in a rice stubble field were dug up to search for hoarded grain. Mice were still numerous at this time, but surface grain was becoming scarce. Therefore, if mice did store food, this seemed a likely time to do it. No stores were found.

2.4. DISCUSSION

The present study showed that house mice on cereal farms in the MIR are opportunist feeders, whose diet reflects changes in available foods, and is subject to considerable seasonal and habitat variation. The high grass seed and cereal grain content of the diet was similar to diets reported by many previous authors for mice in cultivated fields. (Naumov 1940; Sakhno 1957; Whitaker 1966; Houtcooper 1978; Smiet *et al.* 1980; Fulk *et al.* 1981). Although invertebrates and green plant tissue were frequent diet items, the volume contribution of both these foods in the diet was small.

A correlation between food supplies and timing of breeding has been reported previously for house mice (Newsome 1969a; Newsome and Corbett 1975; King 1982; Redhead 1982). A causal relationship between available food supplies and timing and intensity of breeding was strongly suggested by the results of this descriptive study. A diagram which models the apparent relationship between food supply, diet and breeding intensity is presented in Figure 2.12. Post-winter breeding did not begin until about a month after grass seeds reached the milk-ripe stage and were eaten by the mice. This occurred in different crop fields in different months. Peak breeding occurred soon after the cereal grain reached the the milk-ripe stage. Once the crops

were harvested breeding intensity declined.

A decline in breeding beginning immediately after harvest was also reported by Redhead (1982). After harvest, cereal grain is still plentiful, due to the large amounts spilt, and the mice eat a diet consisting mainly of this grain for several months. Over this period breeding ceases. When the grain supply becomes scarce, mice eat a mixture of foods, including dicotyledon seeds and plant vegetable tissue. It is proposed that over the period breeding declines, and during the non-breeding season, the food supplies are limiting for breeding, because they are inadequate in either energy or in particular nutrients. Breeding does not begin again until about a month after fresh grass seeds reach the milk-ripe stage, in the following spring or summer, and it is proposed that this is a causal relationship, with the fresh grass seeds supplying the nutrients or energy that were previously lacking in the diet.

Four possible limiting factors in the diet in the non-breeding season are now discussed.

i) Energy. An energy shortage is the most obvious potential limiting factor, due to the scarcity of seeds in the fields during the non-breeding season. The decline in breeding intensity, however, began immediately after harvest, while spilt grain was still plentiful, which indicates that while an energy shortage may have been one factor limiting breeding, it cannot have been the factor causing the initial decline.

ii) Protein. The minimum protein requirements for house mouse reproduction are not known (See Section 4.1), but it seems likely that the diets eaten by mice in stubble fields, and in fields with crops in the early growing stages, were so low in protein that breeding may have been limited. Samples of wheat and barley

had protein contents of 13.2% and 12.6% respectively. Samples of rice and sorghum were still lower, at only 7.2% to 8.8% for rice, and 9.9% for sorghum. The protein quality in cereal grains is poor, due to an imbalance in their amino acid profile, and lysine is the first limiting amino acid, (Food and Agricultural Organization 1970; Mertz 1974; Pomeranz 1974; Grist 1975; Clark 1978). Non-seed plant tissue has an even lower in protein content, with leaves usually under 5% protein (Food and Agricultural Organization 1970). Milk-ripe grass seeds have a higher protein content than cereal grains, and a sample of milk-ripe barley grass seeds collected from a wheat field in October, was 21.0% protein, and a sample of milk-ripe barnyard grass collected from a rice field in January was 13.0% protein. Some dicotyledon seeds have a higher protein content, usually around 20%, and invertebrate tissue may contain up to 50% protein (Food and Agriculture Organization 1970).

The high frequency of occurrence of invertebrate tissue in the stomachs of mice, suggests that this food is important to the mice. Invertebrate tissue not only has a high protein content, but this protein also has a high lysine content, which makes it complementary to the protein from grass seeds and cereal grain. Therefore, the inclusion of even small amounts of invertebrates in the mice's diet might considerably improve its protein quality.

The diet eaten by mice in the stubble fields, consisted mainly of cereal grain, and therefore would have been low in protein, particularly in the rice stubble habitat. The diet eaten by mice in late winter and early spring in wheat fields, was high in vegetable tissue and so would also have been low in protein. But once milk-ripe grass seeds were included in the diet, the protein content would probably have increased.

iii) Vitamin A. Carotene precursors of vitamin A are present in green plant tissue, such as the wheat flower buds eaten by mice in winter and early spring, and also in milk-ripe grass seeds and cereal grains. In contrast, mature grass seeds and cereal grains, with the exception of sorghum grain, contain negligible quantities (Dam and Søndergaard 1964; Green 1970; Grist 1975). Therefore, the proposal by Ward (1981) and Redhead (1982), that infertility caused by inadequate dietary vitamin A is a cause of seasonal breeding, seemed applicable to the mice in stubble fields, because they ate a diet of mature grain, with little supplementary green food.

iv) Fertility stimulants and inhibitors. It has often been proposed that the breeding of small mammals may be triggered by chemicals present in green plant tissue (Bradbury 1944; Reichman and Van de Graaff 1975; Negus and Berger 1977; Negus *et al.* 1977; Swanepoel 1980; Lam 1983; Nelson *et al.* 1983). One chemical which has been isolated and investigated is 6-methoxybenzoxalinone (6-MBOA), a chemical found in fresh green vegetation but not in browned-off vegetation. 6-MBOA triggers aseasonal breeding in the montane meadow vole *Microtus montanus* (Berger *et al.* 1981; Sanders *et al.* 1981). Rose *et al.* (1982) tested 6-MBOA on field populations of several rodent species. They found that *Sigmodon hispidus* and *Microtus pennsylvanicus* came into breeding condition, when this chemical was added to their diet, but in contrast, in house mice 6-MBOA affected neither litter weights, number of females pregnant nor number of males with sperm.

Olsen (1981) found that a plant growth hormone, gibberellin A_3 (GA_3), has a stimulatory effect on the breeding of wild-strain house mice. Olsen tested the effect of GA_3 on the breeding performance of caged, wild-strain house mice which were collected from the MIR. The GA_3 was added to the drinking water in concentrations ranging from 10^{-4}M to 10^{-7}M. Concentrations of

10^{-6}M and 10^{-7}M caused more females to breed than females from control pairs given untreated drinking water ($p<0.01$). These findings were of particular interest in view of the finding in the present study of the onset of breeding soon after milk-ripe seeds are included in the diet. Milk-ripe seeds of perennial rye grass (*Lolium perenne*) and milk-ripe barley grain (*Hordeum vulgare*) and wheat grain (*Triticum aestivum*) which are the same genera as the spring grass seeds eaten by mice in wheat and barley fields, have high GA_3 activity. (Murakami 1960; Stoddart 1965; Mounla and Michael 1973). The activity of gibberellic acid is also high in milk-ripe rice grain, at 4.5 to 7.0 µg GA_3 equivalents (Murakami 1960 and 1977; Osada *et al.* 1973). The active gibberellic acid in rice grain is GA_{19} but this has a similar activity to GA_3 (Kurogoshi *et al.* 1979). The GA_3 activity in seeds drops as they mature. Fully ripe grass seeds and cereal grains have near zero quantities of free GAs, and where they do occur, they are present as biologically inactive structures (Jones and Stoddart 1977; Graebe and Ropers 1978).

Oestrogenic compounds in some plants are known to produce temporary or permanent infertility in livestock eating them (Shutt 1976), and laboratory mice have been shown to be susceptible to these effects (Dohan *et al.* 1951; Munford and Flux 1961; James and Foote 1972). A range of other antifertility agents also exist in plant foods (Farnesworth *et al.* 1975a,b; Berger *et al.* 1977). Some of these may be present on mouldy seeds or in dicotyledon seeds and leaves, and these foods form a larger proportion of the mice's diet in the non-breeding season.

In summary, the diet of mice apparenty improved in several respects, just prior to the onset of breeding. When grass seeds and cereal grains reached the milk-ripe stage, not only did they supply abundant high-energy food, but their nutrient content probably increased the dietary intake of protein, vitamin A, and

GA_3, and possibly other nutrients or stimulants also.

Pryor and Bronson (1981) pointed out that it is not clear whether energy or particular nutrients are limiting for breeding. Bronson's (1979) suggestion that seasonal changes in specific nutrients are not likely to be a normal cause for seasonal breeding, because of the broad range of diets acceptable to house mice, is not supported by the findings described in this chapter. Wunder (1978) suggests that food quality will be less important for seed eaters than for herbivores because 'Presumably once a seed is formed its composition does not change greatly', and Hansson (1979) made a similar suggestion. This assumption led both authors to concentrate on the available food energy, rather than the nutrient composition of food, when formulating hypotheses relating the breeding performance of seed eaters to their food supply. But there are several reasons against accepting this suggestion. Not only do milk-ripe seeds often have a higher content of GA_3, vitamin-A precursors, and protein, than mature seeds, but also, many vitamins are extremely labile (Green 1970), and exposure of mature seeds to heat and sunlight in the field may reduce their vitamin content. In addition, water-soluble vitamins and minerals may leach out of seeds if they are soaked (Davis 1970). Germination of seeds also causes rapid changes in their nutritional quality. Their dry weight decreases and the protein to carbohydrate ratio increases (Lemar and Swanson 1976; Miller 1977; Hamad and Fields 1979; Lorenz 1980). The concentration of GA_3 (Murakami 1960; Groat and Briggs 1969; Osada *et al.* 1973; Jones and Stoddart 1977) and 6-MBOA (Pinter and Negus 1965; Sanders *et al.* 1981) also increases during germination, and some vitamins, especially vitamin-A precursors and most B-vitamins qualitatively increase too (Chedelin and Lane 1943; Lemar and Swanson 1976; Miller 1977; Lorenz 1980). Therefore diets with germinating or milk-ripe seeds may be superior nutritionally to those with mature seeds, and diets with fresh mature seeds may be

superior to those with stale seeds. In addition, the species of seed available to seed eaters may change, and the nutritional quality of different kinds of seeds varies widely (Food and Agricultural Organization 1970). Further, changes in temperature, soil moisture, or farming practices alter the availability of different types of seeds and the extent to which house mice include them in their diet (Table 2.4, Figure 2.7) and these changes are expected to affect reproduction because the breeding performance of caged house mice has been shown to be affected by the kinds of seeds they eat (Deol and Truslove 1957; Pryor and Bronson 1981).

In most habitats and seasons mice supplemented their seed diet with various quantities of alternative foods, mainly green plant and animal tissue. These supplements may have been be a valuable source of nutrients. Only in a few habitats were the mice found to restrict their diet largely to a single grain type for extended periods, and it is during these periods that the liklihood of particular nutrients being inadequate for breeding seems strongest. The most obvious example is the diet of mice in the rice fields for April to August. Over these five months, mice ate more than 90% rice. Here a clear likelihood that particular nutrients may have been limiting exists.

The data from the present study on available food supplies in rice stubble fields in the winter of 1980, suggest that the population crash recorded in late winter may have been caused by starvation. Food supplies present on Farm J in June were sufficient to feed the mice for about one week, as Redhead (pers. com.) estimated density of mice to exceed 100 mice/ha. The lower body fat content of the mice on Farm J may have been caused by the scarce food supplies, as a reduced food intake could have forced them to metabolize some of their fat deposits. Their fat levels were still fairly high though, even when food was so

superior to those with stale seeds. In addition, the species of seed available to seed eaters may change, and the nutritional quality of different kinds of seeds varies widely (Food and Agricultural Organization 1970). Further, changes in temperature, soil moisture, or farming practices alter the availability of different types of seeds and the extent to which house mice include them in their diet (Table 2.4, Figure 2.7) and these changes are expected to affect reproduction because the breeding performance of caged house mice has been shown to be affected by the kinds of seeds they eat (Deol and Truslove 1957; Pryor and Bronson 1981).

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scarce, which suggests that body fat levels are not a good indicator of food supplies.

Redhead (1982) reviewed the literature on factors affecting body fat stores in rodents. He found that body fat stores are negatively correlated with breeding activity. Such a negative correlation was found for high density populations of house mice in two studies conducted in haystacks (Rowe *et al.* 1964; Newsome 1971), and in two studies conducted in enclosures (Strecker and Emlen 1953; Lidicker 1976). Obese mice survive longer than thin mice when they are deprived of food (Cuendet *et al.* 1975), and Redhead suggests obesity may be an adaptation to limited food supplies. Evidence that obesity in house mice does not necessarily reflect an abundance of food was presented in Strecker and Emlen's (op. cit.) study. They found mice in an enclosure with a limited food supply were very fat, while mice from a control enclosure with unlimited food and a higher per capita food consumption were not so fat. Strecker and Emlen claim that Robertson *et al.* (1934) showed that experimental reduction of the food intake of laboratory mice leads to an increase in fat deposition, but inspection of Robertson's paper does not support this claim. In the winter of 1982, however, when mice in rice stubble fields had moderately high body fat levels (Table 2.6), evidence that these mice may not have had a plentiful food supply, comes from the finding of six torpid mice in a rice stubble bank (W. Price pers. comm.). Torpidiy is usually associated with food deprivation in house mice (Hudson and Scott 1979). Presumably such torpor reflected a need for energy conservation, implying a shortage of available food. The fat levels found in the present study are in agreement with Redhead's finding of a negative correlation between breeding activity and body fat content. Fat levels were lower in autumns when the breeding season was extended.

A possible role for temperature as a limiting factor for breeding, appeared restricted to the four coldest months of 1979, June through September, as there was no indication of any correlation between environmental temperature and breeding intensity during the eight month breeding season. It is, however considered unlikely that low temperatures were the only factor preventing breeding during these four cold months, as Redhead (1982) recorded almost continuous breeding in these months in 1978, when the mean minimum temperature over this period was only 0.3°C higher than the mean for 1979. But temperature may affect the mice's response to low-quality diets. Pryor and Bronson (1981) found mice can breed well on a diet of pure wheat grain if they were in a warm environment (23°C), but not in a cold one (3°C).

It is possible that a water shortage may have caused suppression of breeding in the wheat and barley stubble fields in summer, as these habitats were very dry. Although mice can get sufficient metabolic water for survival from a diet of dry seeds (Fertig and Edmonds 1969), it is unlikely this source would be adequate to meet the demands of gestation or lactation. Schmidt-Nielsen (1975) found that the production of milk is a major drain on the water resources of rodents, and that this is increased by a large litter size. Newsome's (1970) suggestion, that breeding may be limited by a lack of nest sites when soils are too dry to allow burrowing, was inapplicable to MIR wheat and barley fields, because extensive burrow systems are built in spring in these habitats, and remain available through the summer. In the sorghum and rice stubble fields there was no water shortage, as the soils remained damp or wet, so there was never a water shortage in these habitats.

Social regulation of breeding seems unlikely to have occurred in the wheat and barley fields, because mice were in low numbers when breeding declined in early summer. In contrast, mouse num-

bers were high in the rice and sorghum crops at the time breeding declined, and so a role for social suppression of breeding is more likely here. Redhead (1982) developed a model to describe how social suppression of breeding may operate in rice stubble fields and this is discussed in detail later in this thesis (Section 5.1).

Table 2.1. A summary of the results of previous studies of the diet of house mice in cultivated and uncultivated habitats. N = number of stomachs or faecal samples analysed.

Diet by volume	Diet by season	N	Habitat	Location	Reference
Cultivated habitats					
Seeds major food, mainly cereal grains and grass seeds, with smaller quantities of dicotyledon seeds. Smaller contributions made by green vegetation tuberous roots, fruits berries, insects and other invertebrates.	Spring: early ripening grass seeds and germinating seeds left from previous autumn. Summer: mainly cereal grains especially oats, rye, wheat and barley. Autumn: cereals such as corn and sorghum, and some dicotyledon seeds, such as legume and composite seeds. Winter: Autumn seeds which had been stored in mounds by mice for winter food.	243	cultivated farmland	Russian Ukraine	Naumov (1940)
Mainly cereal grains, grass seeds and weed seeds, Smaller quantities of green vegetation and invertebrates, mainly insects and larvae.	Seeds important all year round, with cereal grains important at sowing and harvest times. Green vegetation increases in summer, especially in diet of pregnant and lactating females.	385	cultivated farmland	Russia Voroshilov Province	Sakhno (1957)

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Table 2.1. cont.

Diet by volume	Diet by season	N	Habitat	Location	Reference
Grass seeds 28.7%, mainly Setaria sp. Cereal grains 22.0%, mainly corn and wheat. Animal tissue 24.1%, mainly caterpillars. Other seeds 12.6%. Other plant tissue 12.6%.	Spring: cereal grains 26% mainly wheat and corn. Grass seeds 6%, other seeds 5%, and other plant material 10%. Animal tissue 46%. Summer: cereal grain 24%, mainly wheat. Grass seeds 11%, other seeds 7%, and other plant material 14%. Animal tissue 29%. Autumn: cereal grains 11%, mainly wheat. Grass seeds 32%, other seeds 9%, and other plant material 16%. Animal tissue 14%. Winter: cereal grains 28%, mainly corn. Grass seeds 25%, other seeds 13%, and other plant material 8%. Animal tissue 9%.	478	cultivated weedy and grassy fields	Indiana U.S.A.	Whitaker (1966)

(continued over page)

Table 2.1. (cont.)

Diet by volume	Diet by season	N	Habitat	Location	Reference
Animal tissue 26.8%, mainly caterpillars. Setaria sp. grass seeds 27.7%. Miscellaneous vegetation 19.6%. Corn grain 15.1%. Soybeans 3.0%. Unidentified 7.8%.	Spring: corn 34%, soybeans 33%, miscellaneous vegetation 13%, and animal tissue 19%, mainly caterpillars. Summer: corn 10%, soybeans 2%, miscellaneous vegetation 19%, fungal spores 4%, grass seeds 18%, and animal tissue 37%, mainly caterpillars. Autumn: corn 11%, soybeans 4%, miscellaneous vegetation 20%, grass seeds 39%, and animal tissue 23%. Winter: corn 42%, soybeans 2%, miscellaneous vegetation 13%, grass seeds 33%, and animal tissue 9%.	281	corn and soybean fields	Indiana U.S.A.	Houtcooper (1978)
Seeds major food, mainly wheat and rice grain. Also insects and green sugarcane plant tissue.	Spring: mainly wheat and rice grain, and smaller quantities of weed seeds and insects. Summer: mainly rice grain plus a small quantity of insects	136	sugarcane fields	Pakistan	Smiet *et al.* (1980)

(continued over page)

Table 2.1. (cont.)

Diet by volume	Diet by season	N	Habitat	Location	Reference
	Autumn: nearly all unidentified material, plus a small quantity of insects.				Smiet *et al.* (cont.)
	Winter: mainly insects and sugarcane plants, plus a small amount of rice grain.				
Rice grain about 50%. Smaller quantities of wheat grain and insects.	Winter-spring: rice grain 20%, wheat grain 9%, and insects 22%.	63	rice fields	Pakistan	Fulk *et al.* (1981)
	Summer: rice grain 77%, wheat grain 1%, and insects 6%.				
	Early Autumn: rice grain 11%, wheat grain 25%, and insects 12%.				
	Late Autumn: rice grain 84%, wheat grain <1%, and insects 6%.				
Mainly granivorous. Insects <7% of diet.	Mice store grass seeds and cereal grains, such as corn and wheat, in mounds for winter consumption.	–	cultivated fields.	Yugoslavia Rumania	Hamar (1960) and Mikes (1971) (both cited by Sage 1981)

(continued over page)

Table 2.1 (cont.)

Diet by volume	Diet by season	N	Habitat	Location	Reference
Animal tissue 42.5%, mainly insect eggs and larvae. Grass seeds 32.0%. Sugarcane plant 9.8%. Grass stalks 3.0%. Nuts 1.8%. Unidentified material 10.9%.	No seasonal changes apparent.	343	sugarcane fields	Japan	Kami (1966)
Animal tissue 20.2% Nuts 23.3% Grass seeds 14.6% Unidentified material 41.9%	No seasonal changes apparent.	25	gulches adjacent to sugarcane fields	Japan	Kami (1966)
Uncultivated habitats					
Insect 66% Moss sporangia 14.7% Unidentified plant 3.8% Dicotyledon seed 1.6% Leaf, stem and root 0.7%	Spring: only one stomach analysed. Summer: insect 95.4%, dicotyledon seed 4.6%. Autumn: insect 72%, moss sporangia 12%, fungi 13%, other plant 3%. Winter: insect 24%, moss sporangia 38%, fungi 27%, other plant 11%.	80	wet coastal heath	Australia Victoria	Watts and Braithwaite (1978)

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Table 2.1. (cont.)

Diet by volume	Diet by season	N	Habitat	Location	Reference
Soil invertebrates 31.2% Leaves 29.9% Seeds 15.3% Fungi 12.6% Adult insects 9.8% Flowers 1.2% Roots 1.2% Bryophytes 0.9%	Summer: leaf 22%, seed 9%, fungi 26%, invertebrate 40%, and other plant 4%. Winter: leaf 46%, seed 14%, fungi 2%, invertebrate 35%, and other plant 2%.	19	coastal scrub and heath	Australia Victoria	Cockburn (1980)
Larvae of flightless moth *Pringleophaga marioni* 40% to 60%. Plant material 10% to 30%. Also weevils, adult moths, caterpillars and spiders.	Winter: mainly caterpillars. Plant material low in diet. Spring-Summer-Autumn: mainly caterpillars, but less than in winter. Plant material higher than in winter.	405	offshore island	South Africa Marion Island	Gleeson (1981)
Lepidoptera main food. Also mites, centipedes, spiders, isopods, and some plant material.	Not recorded.	450	offshore island heath	Britain Skokholm Island	Berry (1968)
Plant fibres and seed cases. Also insects, spiders and feathers. Relative volumes not recorded.	Not recorded.	34	mostly grazing land	Shetland Islands	Berry and Tricker (1969)

(continued over page)

Table 2.1. cont.

Diet by volume	Diet by season	N	Habitat	Location	Reference
Seeds 56% Animal tissue 45% Other plant tissue 5%	Spring: animal tissue 61%, seeds 46%. Summer: animal tissue 39%, seeds 7%. Autumn: animal tissue 45%, seeds 55%. Winter: animal tissue 65%, seeds 35%.	60	coastal heath and open forest	Australia	Thomson (1979)
Seed 60% **Root 5%** **Green plant 5%** **Debris 4%**	Not recorded	15	inland desert	Australia	Watts (1977)
Seed 58% **Animal tissue 42%** **Also green plant trace.**	March only.	7	abandoned fields	U.S.A. South Carolina	Caldwell (1964)

Table 3.4. Known seed foods recorded in the stomachs of wild-caught mice, and likely and unlikely seed foods, collected in the trapping habitats, and tested on caged mice.

KNOWN SEED FOODS	LIKELY SEED FOODS	UNLIKELY SEED FOODS
Monocotyledons	Monocotyledons	Monocotyledons
Cereal grains	great brome *Bromus diandrus*	blown grass *Agrostis avenacea*
barley *Hordeum distichon*	neverfail grass *Eragrostis setifolia*	couch grass *Cynodon dactylon*
corn *Zea mays*	pigeon grass *Setaria* sp	dirty dora *Cyperus difformis*
oats *Avena sativa*	prairie grass *Bromus unioloides*	paspalum *Paspalum dilatatum*
rice *Oryza sativa*	silky brome *Bromus molliformis*	umbrella sedge *Cyperus eragrostis*
sorghum *Sorghum bicolor*		water couch *Paspalum paspalodes*
wheat *Triticum aestivum*	Dicotyledons	windmill grass *Chloris truncata*
	starchy	
Grasses and rushes		Dicotyledons and fern
barley grass *Hordeum leporinum*	shiny dock *Rumex crystallinus*	
barnyard grass *Echinochloa crus-galli* and *E. colonum*	non-starchy	Australian hollyhock *Lavatera plebeia*
cumbungi *Typha domingensis*		blue crowfoot *Erodium crinitum*
phalaris *Phalaris aquatica* and *P. paradoxa*	Australian carrot *Daucus glochidiatus*	common crowfoot *Erodium cicutarium*
ryegrass *Lolium rigidum*	asterweed *Aster subulatus*	sneezeweed *Centipeda cunninghamii*
wild oats *Avena fatua*	barrel medic *Medicago truncatula*	common sowthistle *Sonchus oleraceus*
	bathurst burr *Xanthium spinosum*	cut-leaf goodenia *Goodenia pinnatifida*
	heliotrope *Heliotropium europaeum*	flax-leaf fleabane *Conyza bonariensis*
		haresfoot clover *Trifolium arvense*
		high sida *Sida trichopoda*

(continued over page)

Table 2.2. Continued

KNOWN SEED FOODS	LIKELY SEED FOODS	UNLIKELY SEED FOODS
dicotyledons	creeping saltbush *Atriplex semibaccata*	jersey cudweed *Gnaphalium luteo-album*
starchy	dandelion *Taraxacum officinale*	nardoo *Marsilea* sp (spore pods)
curled dock *Rumex crispus*	horehound *Marrubium vulgare*	prickly lettuce *Latuca serriola*
narrow-leaf dock *Rumex tenax*	lucerne *Medicago sativa*	small plantain *Plantago varia*
wireweed *Polygonum aviculare*	paddy melon *Cucumis myriocarpus*	starfruit *Damasonium minus*
non-starchy	salsify *Tragopogon porrifolius*	yellow devil's claw *Ibicella lutea*
black-berry nightshade *Solanum nigrum*	wild sage *Salvia verbenaca*	
burr medic *Medicago polymorpha*		
capeweed *Arctotheca calendula*		
Paterson's curse *Echium plantaginium*		
peppercress *Lepidium hyssopifolium*		
quena *Solanum esuriale*		
saffron thistle *Carthamus lanatus*		
spear thistle *Cirsium vulgare*		
subterranean clover *Trifolium subterraneum*		
sunflower *Helianthus annuus*		
tufted bluebell *Wahlenbergia communis*		
variegated thistle *Silybum marianum*		
yellow wood sorrel *Oxalis corniculata*		

Table 2.3. Variance due to within-slide and between-slide sources, for foods in the seven untreated slides made from stomach contents of mice from the barley field habitat in September 1979. Between-slide variance was far higher than within-slide variance for all foods except invertebrates. This food had a higher within-slide variance than the others owing to its larger particle size, which gave it a less even distribution across each slide.

Food	Barley grass seed	Other plant tissue	Rice grain	Invertebrate tissue	Dicotyledon seed
Mean food %	64.6	23.3	1.3	1.2	9.6
Standard deviation	31.4	29.8	2.2	1.9	16.0
Residual* mean square	86.8	95.81	0.1895	52.70	43.76
Total* mean square	934.7	858.1	4.264	100.0	270.3
Within-slide variance %	9.3	11.2	4.4	52.7	16.2
Between-slide variance %	90.7	88.8	95.6	47.3	83.8

* Between-slide mean squares.

Table 2.4. Seeds collected in trap habitas in monthly trap-sessions. x = seed present, X = seed abundant. Underlining signifies a seed is at least 20% of the mice's diet in that month.

2.4a. Wheat fields

Habitat	Crop						Stubble		
Year	1979							1980	
Month	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Apr
Seed type									
Bathurst burr	x								
burr medic	X				x	x	x		
tufted bluebell	x								X
peppercress	x	x		x	x	x	x	x	x
wireweed	x								X
saffron thistle	x	x					x	x	
barley grass				X	x	x			
wheat	x				X	X	X	x	
phalaris					X	X	X	x	
ryegrass					X	X	X		
wild oats					x	x	x		
silky brome					x	x			
cape weed					x	x			
Paterson's curse					x	x			
narrow leaf dock					x				
Australian carrot						x			
barrel medic						x			
blackberry nightshade						x	x		
curled dock						x	x	x	x
spear thistle						x	x		
variegated thistle						x	x		
yellow wood sorrel						x	x	x	x
quena							x	x	
subterranean clover									x

Table 2.4b. Barley fields

Habitat	Stubble						Crop			
Year	1979									
Month	Jan	Feb	May	Jun	Jul	Aug	Aug	Sep	Oct	Nov
Seed type										
barley grass	x	x	x				x	X	X	x
rice							X	x	x	x
barley	X	x	x	x	x	x			X	X
phalaris	X	x							X	X
ryegrass	x	x	x						X	X
Paterson's curse	x									x
saffron thistle	x	x								
variegated thistle	x	x								
spear thistle	x	x	x							
bathurst burr		x	x							
peppercress	x	x	x	x	x					
burr medic		x	x	x	x					
curled dock			x	x	x		x	x		
heliotrope			x	x						
narrow-leaf dock			X	x			x	x		
paddy melon			x	x	x	x	x			
blackberry nightshade							x	x		

Table 2.4c. Channel banks.

Year	1979								
Month	Jan	Feb	Apr	May	Jun	Sep	Oct	Nov	Dec
Seed type									
barley grass	x	x	x			X	x	x	
ryegrass	x	x	x	x			x	x	x
silky brome							x	x	
wild oats	x						x	x	x
narrow-leaf dock					x	x	x	x	x
barrel medic							x	x	x
bathurst burr		x	x				x		
curled dock	x	x	x	x			x	x	x
great brome							x	x	x
heliotrope							x		
tufted bluebell			x	x			x		
wheat (spilt grain)							x	x	x
yellow wood sorrel	x						x	x	x
wild sage							x		
blackberry nightshade		x	x	x				x	
cape weed								x	
paddy melon		x	x	x	x			x	x
Paterson's curse	x	x						x	x
phalaris	x	x						x	x
salsify								x	
saffron thistle		x							
spear thistle	x	x	x	x	x			x	x
variegated thistle								x	
dandelion	x								x
cumbungi	x	x							
barnyard grass	x	x	x	x	x				
wireweed	x	x	x	x					
burr medic	x	x	x	X	X				
rice (spilt grain)			x						
quena		x							
peppercress		x	x	x	X	x			

Table 2.4d. Rice fields.

Habitat	Crop	Stubble										Crop	
Year	1979												
Month	Jan	Feb	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Nov	Dec
Seed type													
barnyard grass	X	X	x	x									
barley grass	x	x	x										x
phalaris	x	x								x	x	x	x
rice		X	X	X	x	x	x	x	x	x	x	x	x
ryegrass	x											x	x
peppercress	x	x	x								x	x	x
paddy melon	x	x	x							x	x		
saffron thistle	x	x	x										
spear thistle	x	x	x										
variegated thistle	x	x	x							x	x		
bathurst burr			x										
blackberry-nightshade		x	x	x									
wireweed			x	x	x								
burr medic	x	x	x	x	x								
curled dock	x	x	x	x	x	x					x		x
narrow-leaf dock										x	x		
yellow wood sorrel									X	X	X		
										x	x		

Table 2.4e. Sorghum fields.

Year	1979						
Habitat	Crop				Stubble		
Month	Feb	Apr	May	Jun	Jul	Aug	Sep
Seed type							
sorghum	X	X	X	X	x	x	x
pigeon grass	x	x	x	x	x		
burr medic	x	x	x	x	x		
barnyard grass	X	x	x				
neverfail grass	x	x					
Paterson's curse	x						

Table 2.5. Food supply in rice bays and on rice contour banks in 1979. Measured by Newsome's method.

Habitat	Date	Number of bins	Available grain g/m^2* ±S.E.
Rice contour bank	27 Feb.	4	105.0±15.3
Unripe rice	27 Feb.	4	18.4±3.0
Rice contour bank	30 March	9	73.5±21.7
Ripe rice	30 March	10	725.2±44.6
Rice stubble, Farm C	1 May	12	31.1±11.0
Rice stubble, Farm J	1 May	8	32.3±7.2
Rice contour bank	20 July	8	< 10
Rice stubble	20 July	12	< 10

* Food supplies are given as the weight of barley grain which would have an equivalent digestible energy content to the available food.

Table 2.6. Food availability measured by quadrat sampling, trap success, body fat contents and breeding intensity in rice stubble fields in winter for four years. Sample sizes for body fat analyses are given in brackets. There were no significant differences in body fat contents between sexes in any sample.

Farm	Year	Rice g/m^2	Numbers % trap success	Male % fat* ±S.E.	Female % fat* ±S.E.	Combined sex % fat* ±S.E.	% adult females pregnant
Farm B	18 June 1980	2.16	39	39.0±2.6 (16)	35.4±3.0 (18)	37.1±2.0 (34)	0%
Farm J	18 June 1980	0.23	14	24.4±2.6 (12)	22.8±2.4 (12)	23.6±1.7 (24)	0%
Farm B	18 August 1980	0.31	2	-	-	-	-
Farm J	18 August 1980	0.16	0	-	-	-	-
Farm J	18 June 1981	112.58	0	-	-	-	-
Farm F	18 June 1982	10.57	31	30.8±2.9 (12)	29.6±2.4 (12)	30.2±1.9 (24)	[illegible]
Farm C	18 June 1982	13.03	35	-	-	-	[illegible]
Farm S	18 June 1983	>500	19	17.9±2.5 (15)	21.1±2.1 (10)	19.2±0.6 (25)	15%
Farm P	18 June 1983	>50	20	-	-	-	20%

* Sample sizes for body fats in brackets.

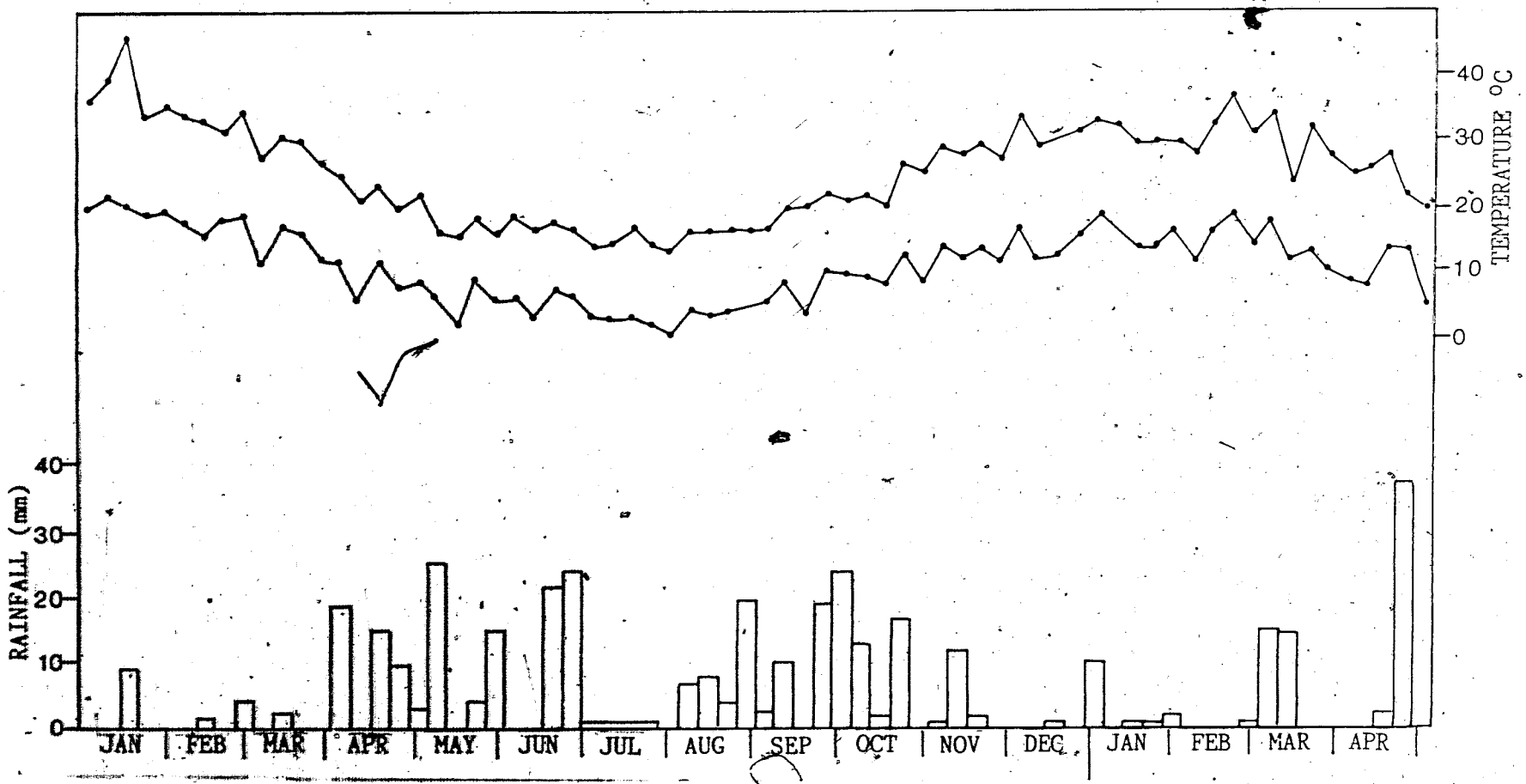
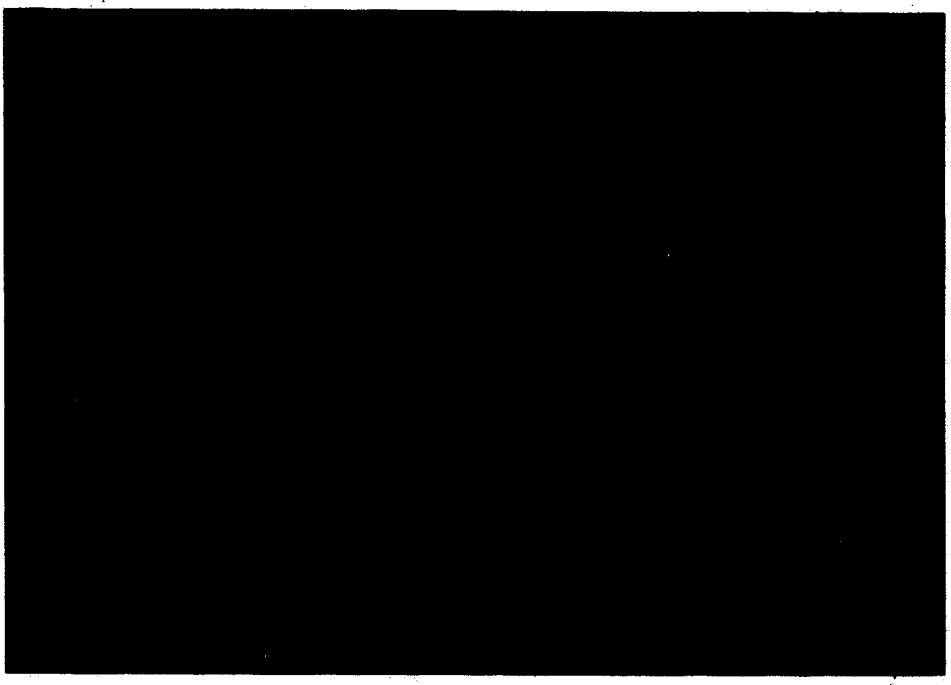


Figure 2.1. Temperature and rainfall data for Griffith NSW over the study period January 1979 to April 1980. Mean maximum and minimum weekly temperatures are given, and total weekly rainfalls.

A

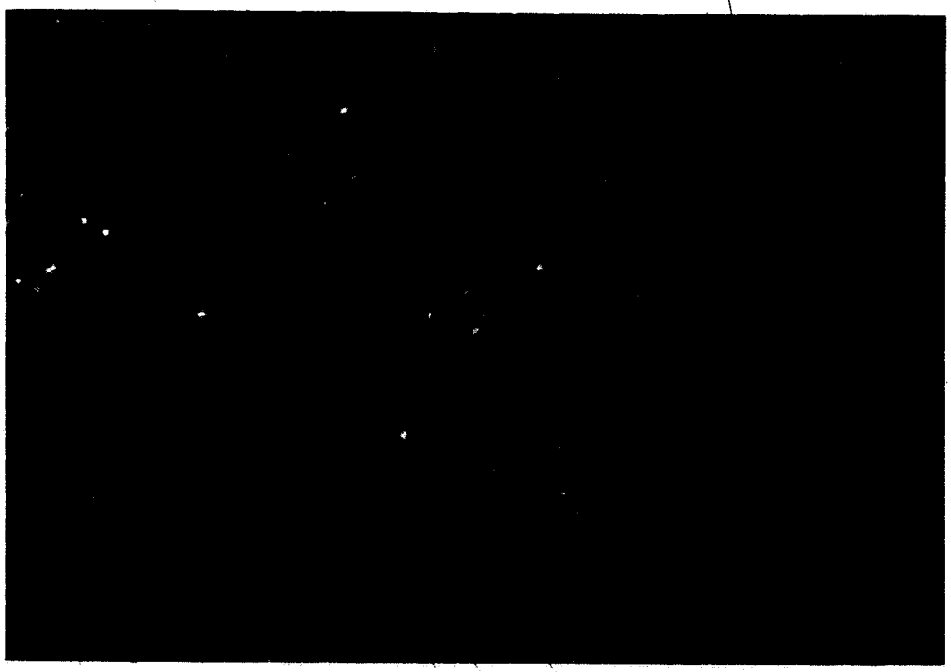


B



Figure 2.2. Photomicrographs of slides of untreated stomach contents viewed under polarized light, magnified to 100 diameters in all photographs. Dicotyledon seeds were usually identified by the structure of the seed coat fragments and the examples shown are A) Peppercress, and B) Narrow-leaf dock. (Cont. over page.)

C



D

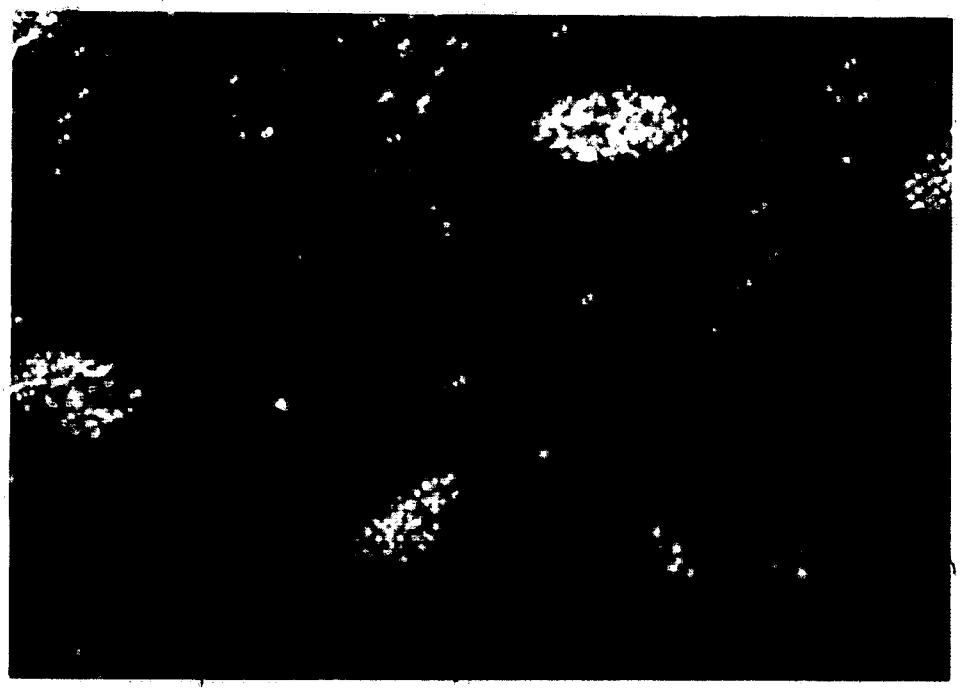


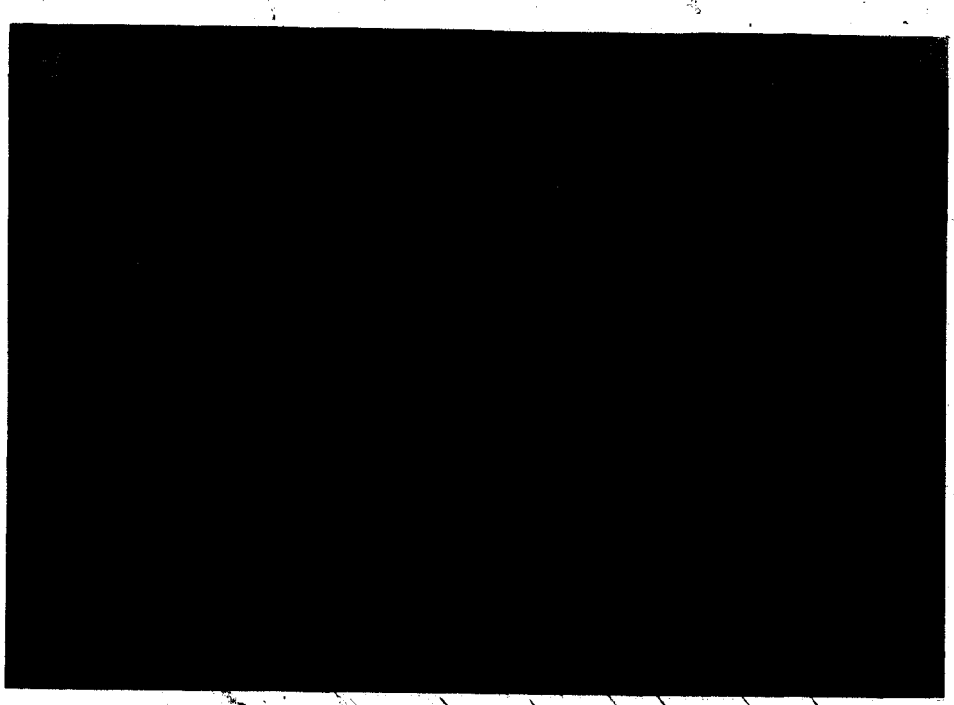
Figure 2.2. Cont. Monocotyledon seeds were usually identified by the the size, shape and cluster pattern of their starch granules, and the examples shown are C) Rice grain, which had small, angular starch granules, D) Barley grass, which had medium-sized round granules clustered into distictive cigar-shaped bundles and E) Wheat grain (shown over page), which had large, sperical granules with a clear, centric bi-refringence cross.

(Cont. over page).



Figure 2.2. Cont. E. Wheat grain.

A



B

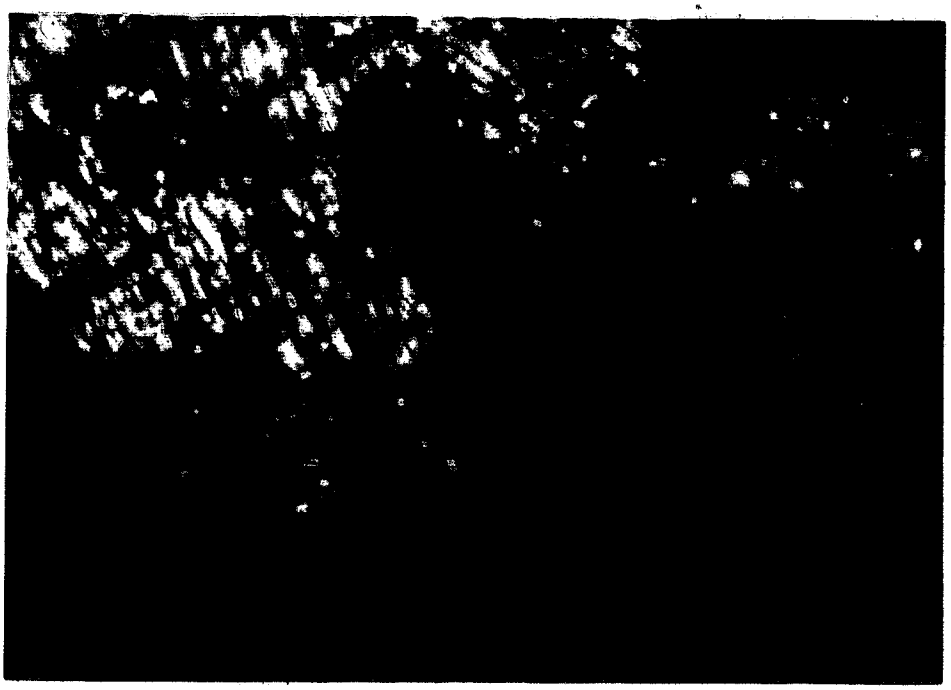


Figure 2.3. Photomicrographs of slides of acid-treated stomach contents, magnified to 100 diameters. A. Barnyard grass seed. B. Rice grain. The starch granules of both these seeds were small and angular and were too similar to be separately identified, but the seed coat fragments of these seeds, viewed in acid-treated slides were quite distinct. The cell walls in fragments of barnyard grass had a highly convoluted appearance, whereas in rice fragements a striated or banded appearance was caused by many faint parallel lines running across them.

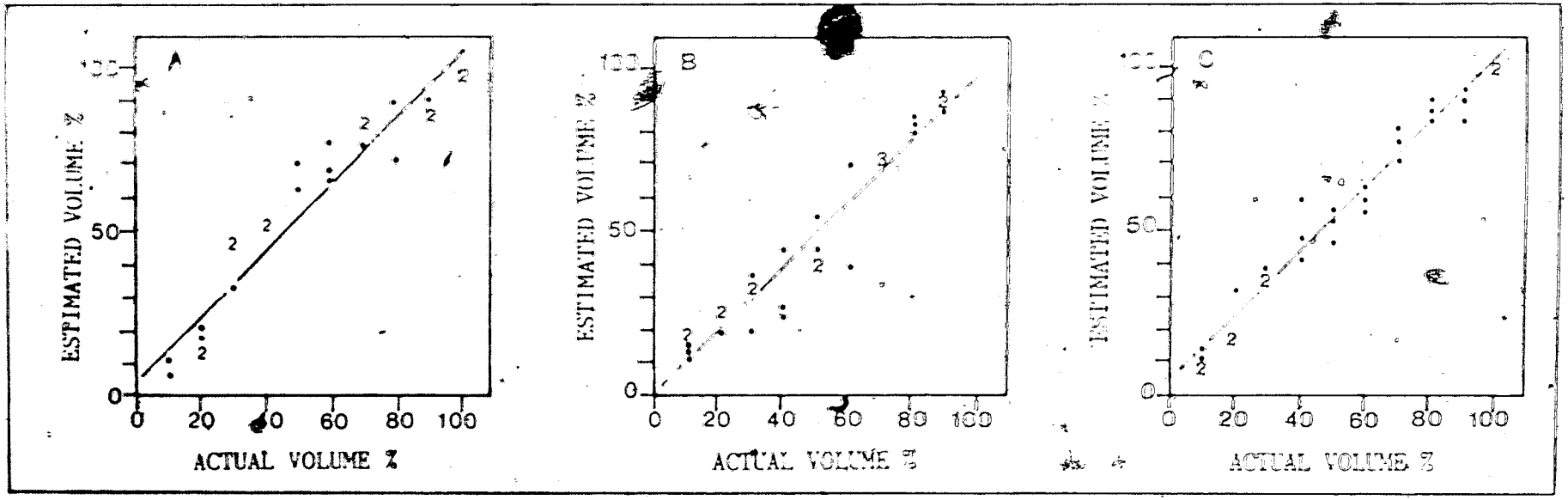
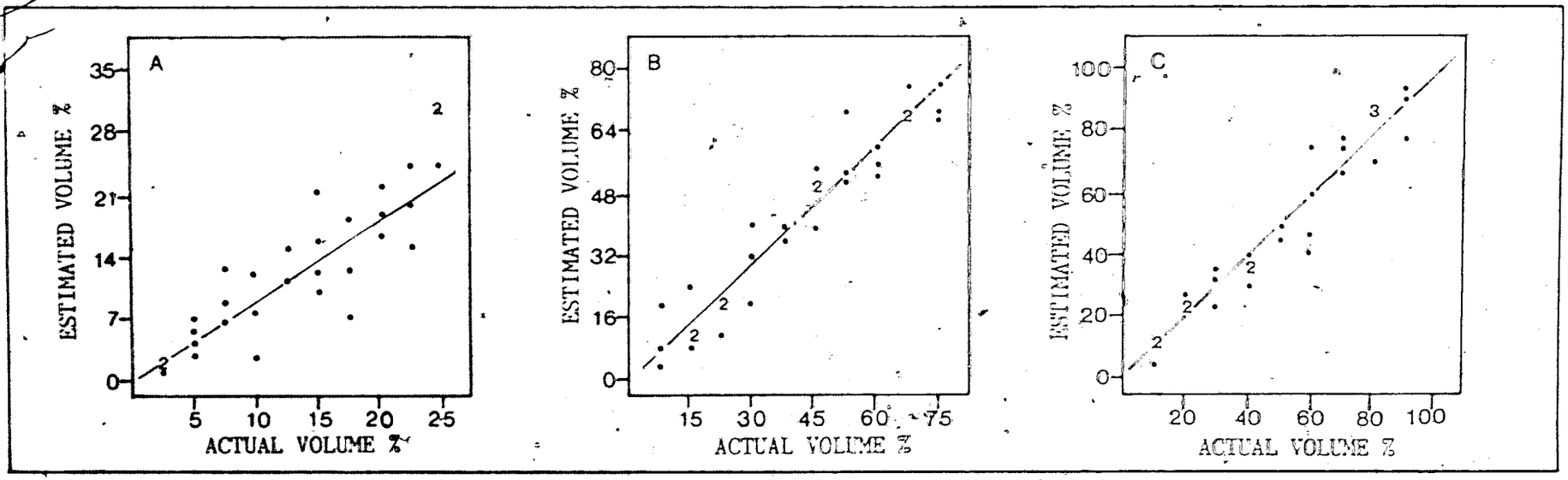
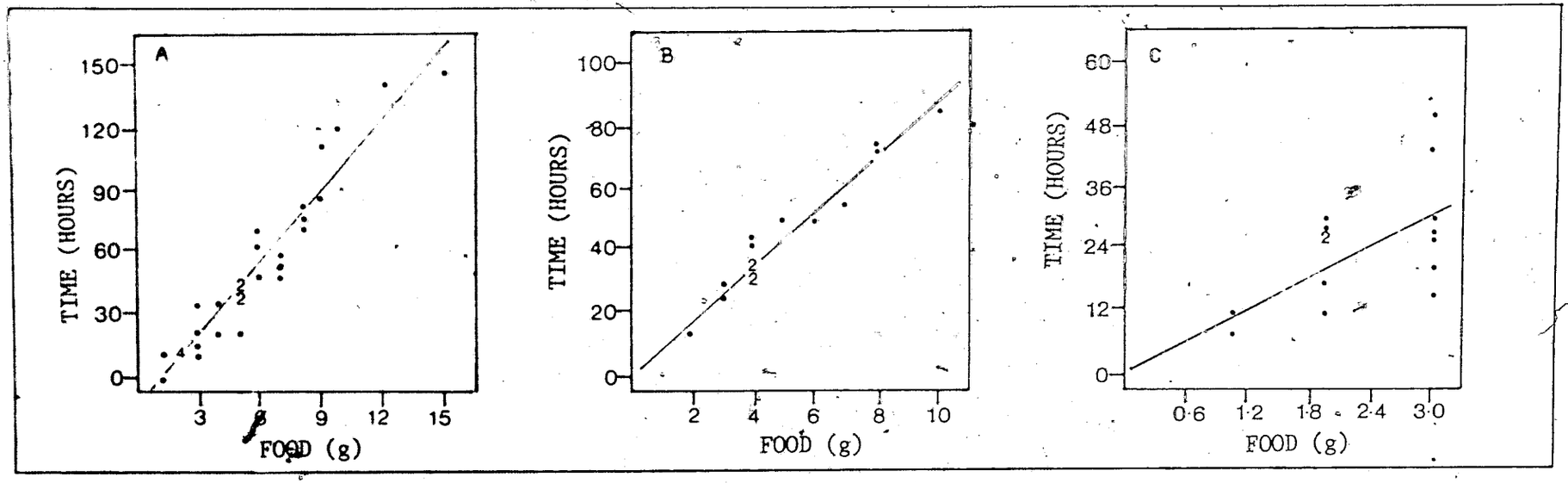


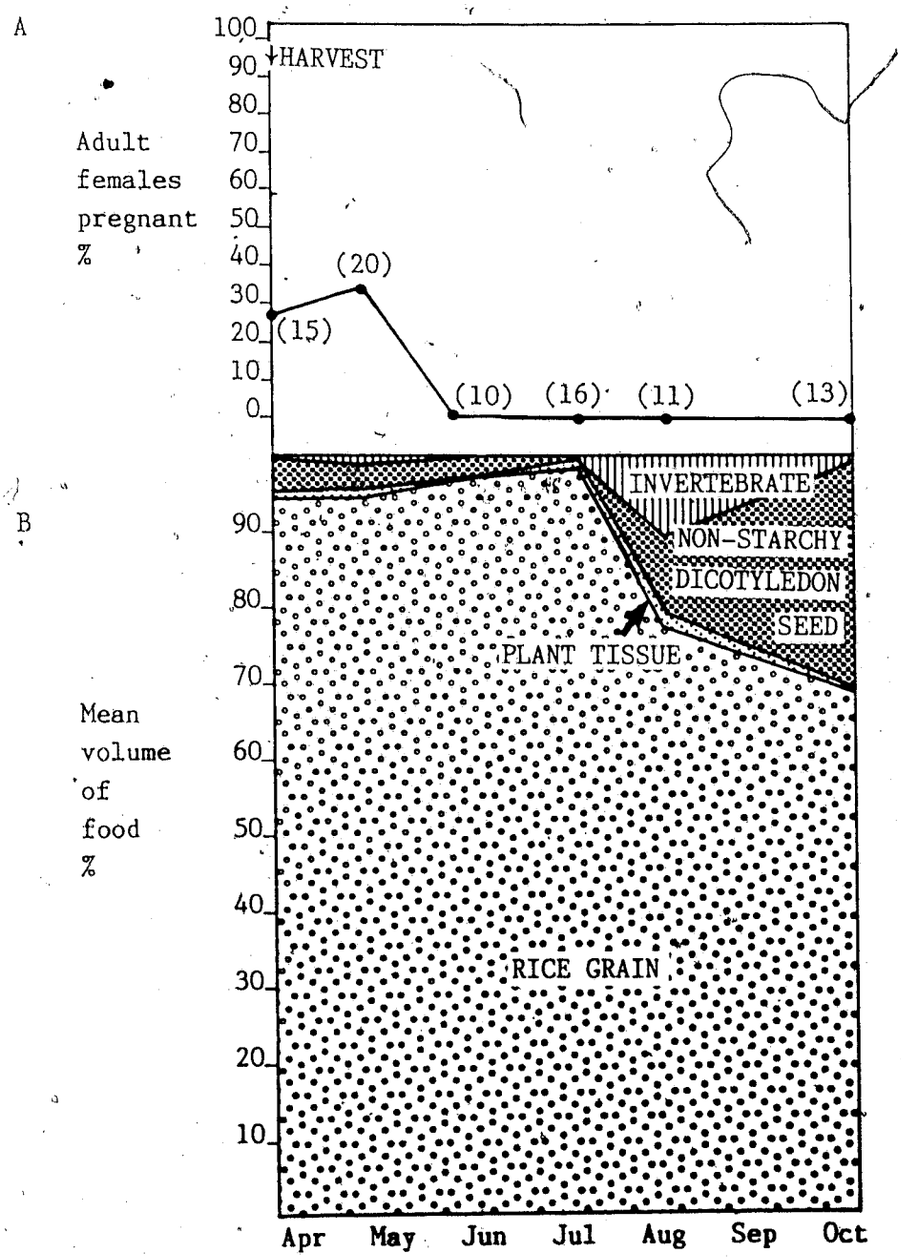
Figure 2.4. Regressions of Estimated percentage volumes of food on Actual percentage volumes. Three series of slides, each for a two-food mixture were tested. A. Estimated % barley in a barley grain and medic seed mixture. The regression line (Est = 1.02 Act + 3.65) accounted for 93.5% of the variance. B. Estimated % wheat plant in a wheat plant and rice grain mixture. The regression (Est = 0.97Act + 1.02) accounted for 93.8 % of the variance. C. Estimated % rice in a rice grain and flour beetle mixture. The regression (Est = 0.99Act + 4.06) accounted for 96.7% of the variance. Numerals indicate superimposed points.



2.5. Regressions of Estimated percentage volumes of food on Actual percentage volumes for a three-food mixture of rice, medic seed and beetle stomach contents. A. The regression for Beetle (Est = 0.98Act − 0.13) accounted for 76.7% of the variance. B. The regression for medic (Est = 1.00Act + 0.55) accounted for 91.3% of the variance. C. The regression for rice (Est = 0.99 Act + 0.20) accounted for 95.4% of the variance

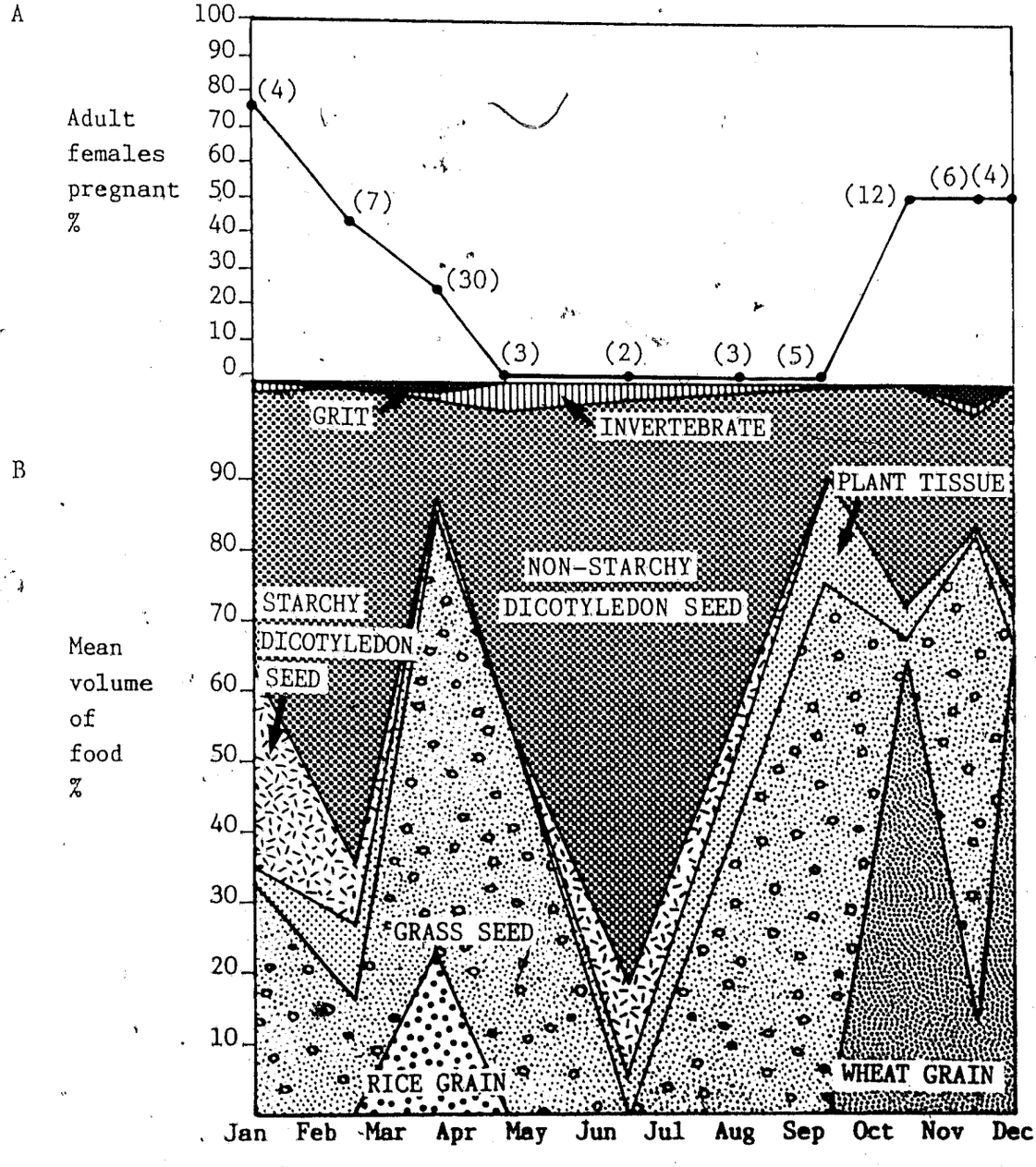


2.6. Calibration of Newsome's method for measuring food supplies in the field. The time a mouse maintained its body weight was regressed on the amount of food it ate. A. March data. The regression (T = 11.45 -11.23) accounted for 93.7% of the variance. B. May data. The regression (T = 8.73A + 0.60) accounted for 96.1% of the variance. C. July data. The regression (T = 10.05A + 1.07) accounted for 56.9% of the variance.



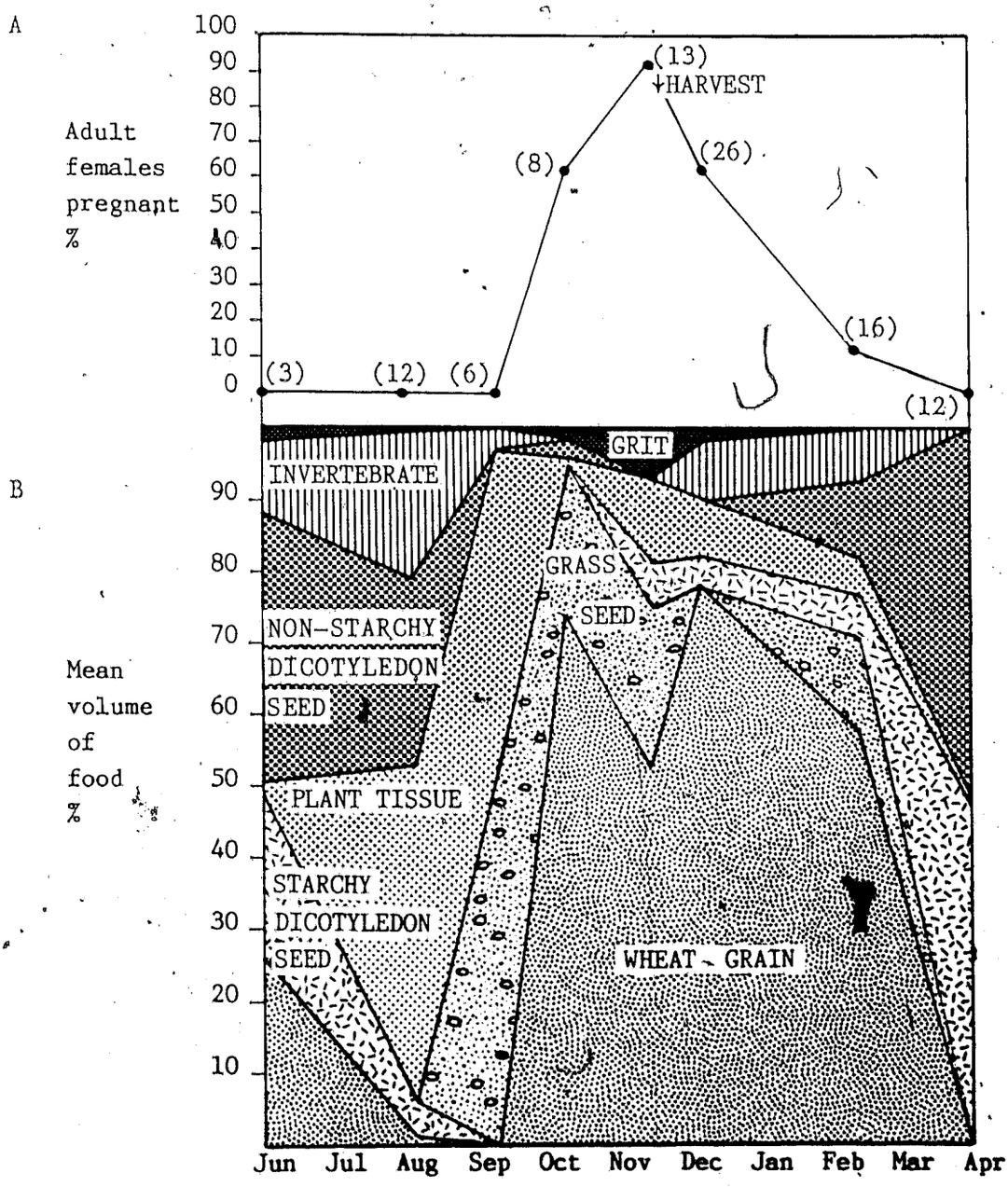
	Apr	May	Jun	Jul	Aug	Sep	Oct
Number of stomachs	21	6	6	7	6	–	4
Main food	R	R	R	R	R	–	R
Mean volume % of main food	94.3	94.2	96.9	98.2	77.3	–	69.0
± standard error	1.7	1.8	2.1	0.6	7.0	–	23.1

Figure 2.7a. Breeding (A) and diet (B) of mice in rice stubble fields: April to October 1979. Adult female sample sizes in brackets. Food symbol: R = rice.



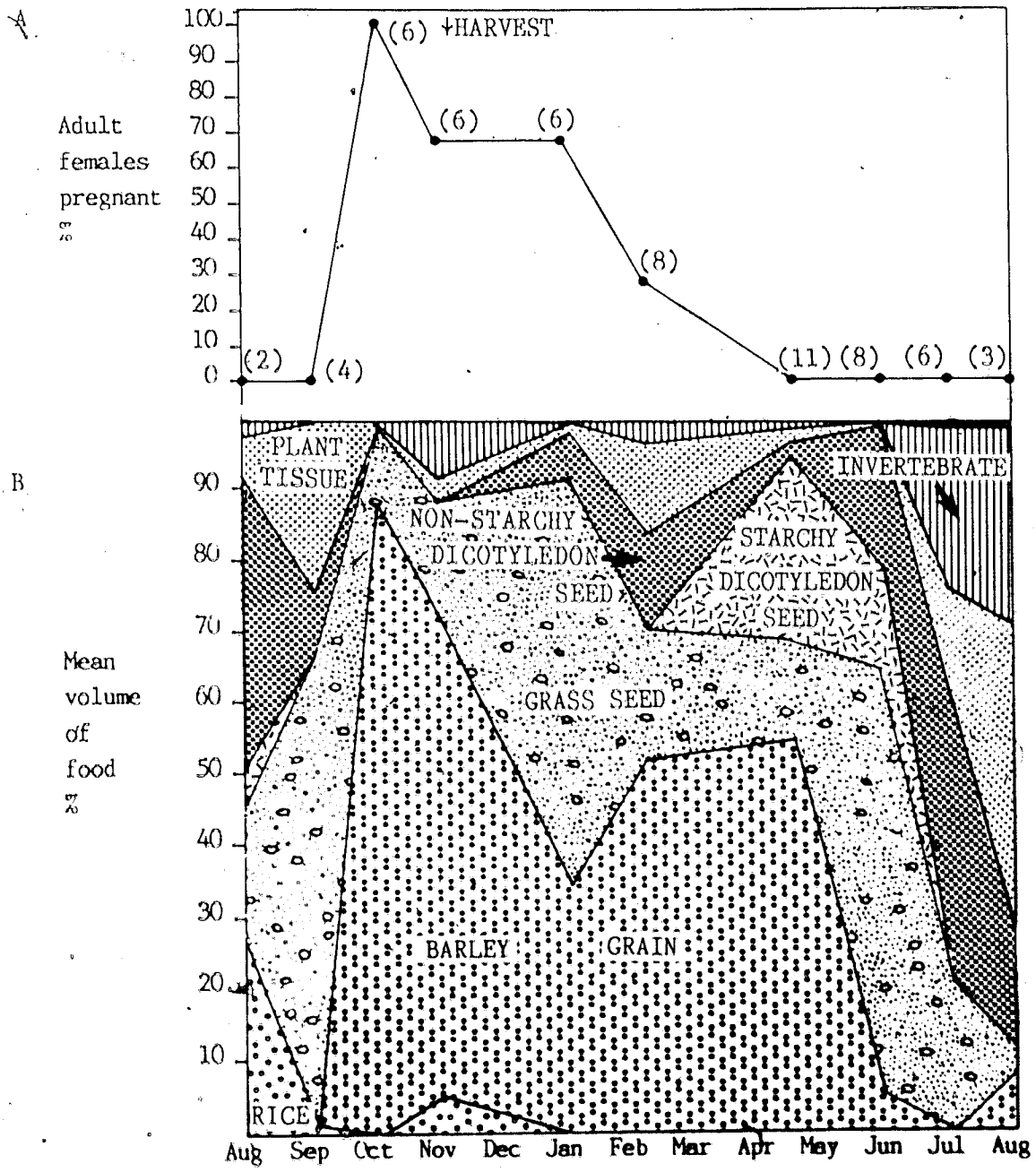
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Number of stomachs	6	–	12	6	6	5	–	–	6	8	10	6
Main food	GS	–	NDS	GS	NDS	NDS	–	–	GS	GS	GS	WG
Mean volume % of main food ± standard error	35.5	–	51.2	62.1	39.3	78.0	–	–	76.6	63.7	59.1	64.0
	16.9	–	11.1	15.8	13.1	14.0	–	–	10.4	17.0	13.4	20.3

Figure 2.7b. **Breeding (A) and diet (B) of mice on channel banks: January to December 1979. Adult female sample sizes in brackets. Food symbols:** GS = grass seed; NDS = non-starchy dicotyledon seed; WG = wheat grain.



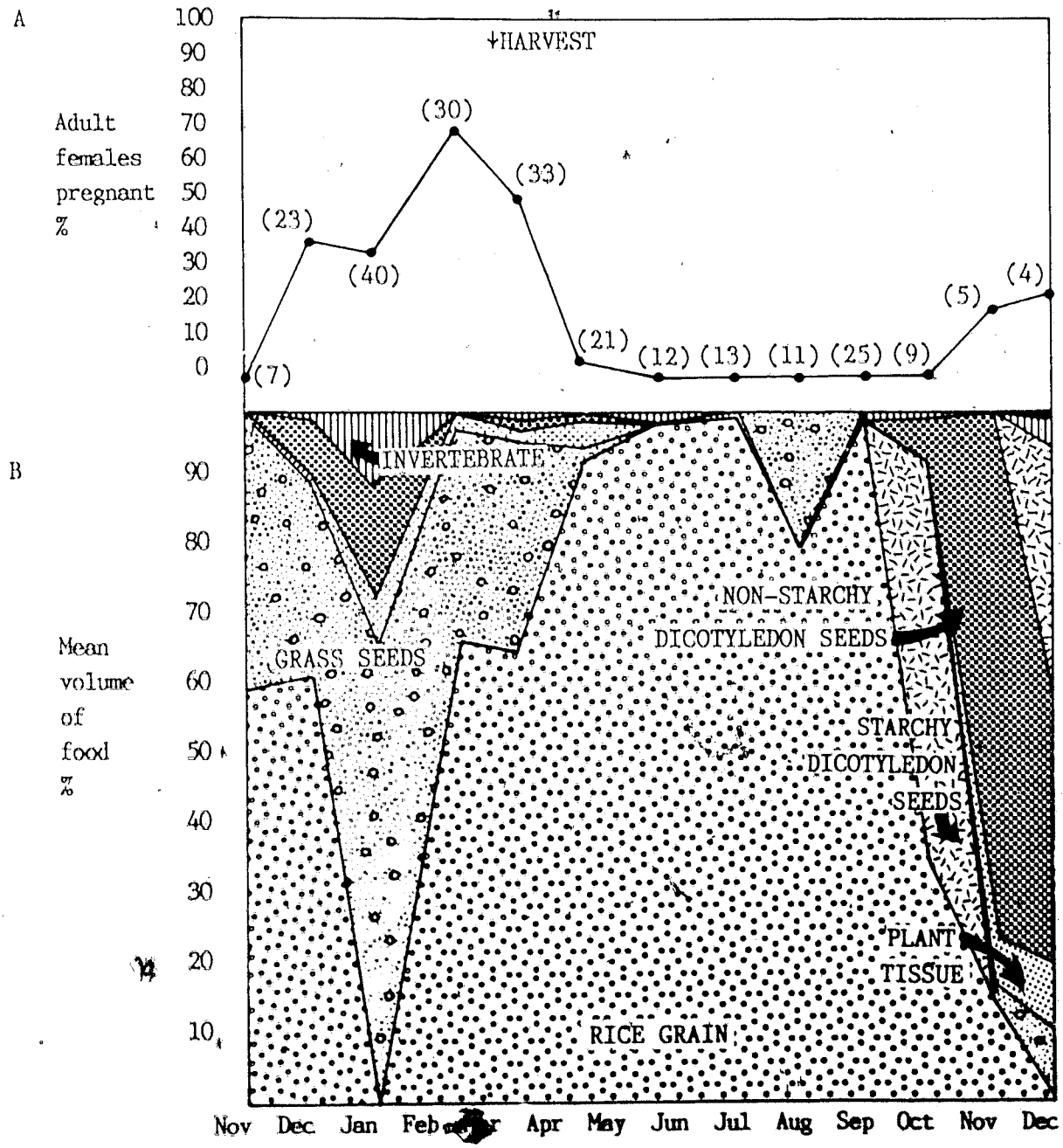
Number of stomachs	6	–	12	6	8	18	12	–	5	–	6
Main food	DS	–	PT	BGS	WG	WG	WG	–	WG	–	WW
Mean volume % of main food ± standard error	36.3	–	45.6	52.6	73.2	52.5	77.9	–	58.1	–	46.8
	18.7	–	11.3	16.4	13.6	8.6	10.2	–	14.8	–	13.4

Figure 2.7c. **Breeding (A) and diet (B) of mice in wheat fields: June 1979 to April 1980. Adult female sample sizes in brackets. Food symbols: DS = dicotyledon seed; PT = non-seed plant tissue; BGS = barley grass seed; WG = wheat grain; SDS = starchy dicotyledon seed.**



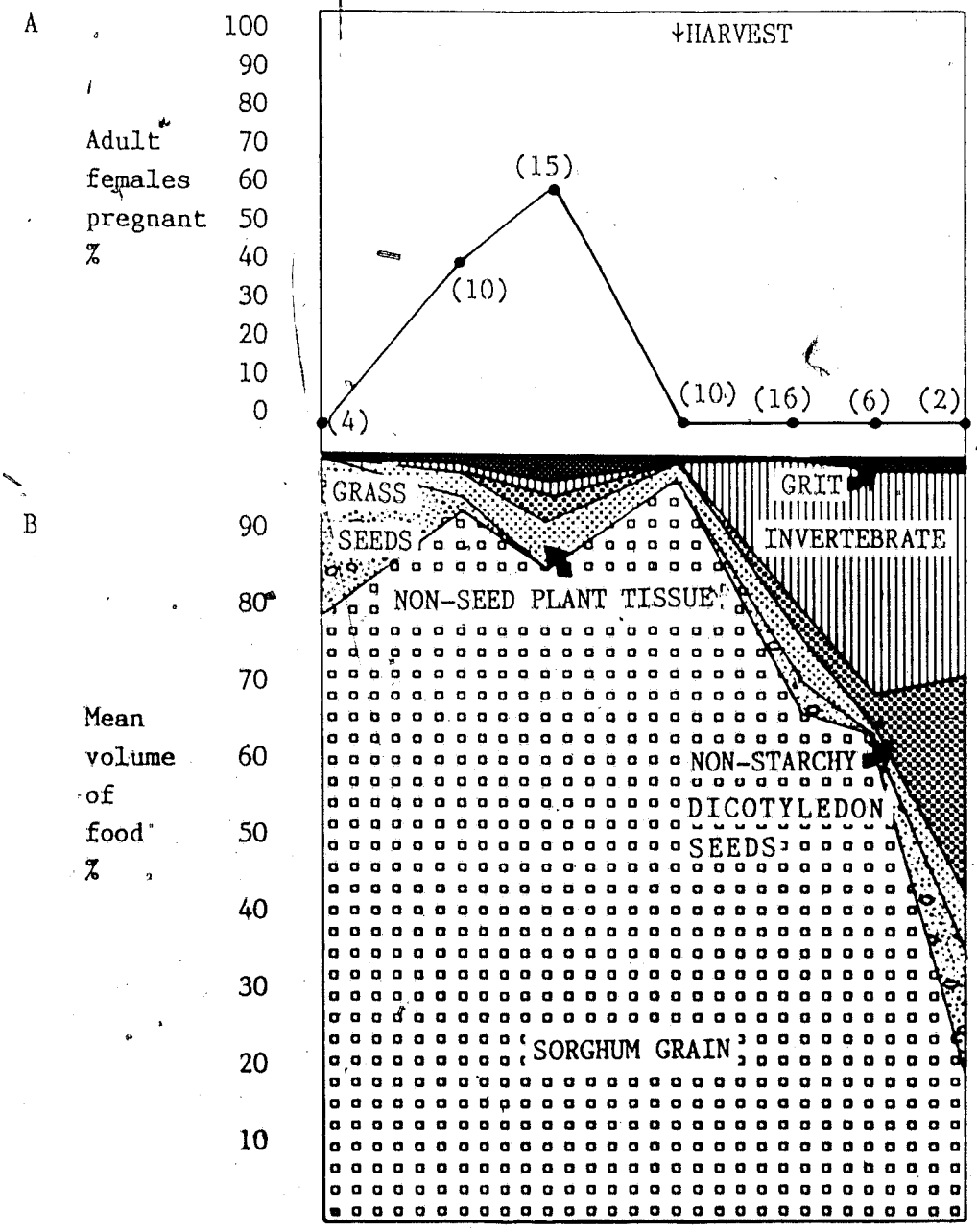
Number of stomachs	6	7	6	9	–	10	6	–	–	7	7	10	4
Main food	NDS	BGS	BG	BG	–	PGS	BG	–	–	BG	GS	I	PT
Mean volume % of main food ± standard error	39.6	64.6	88.2	66.7	–	57.0	52.1	–	–	54.6	58.3	23.5	26.6
	13.7	11.9	6.7	10.6	–	8.9	16.0	–	–	17.4	14.2	8.8	15.4

Figure 2.7d. **Breeding (A) and diet (B) of mice in a barley field: January to December 1979. Adult female sample sizes in brackets. Food symbols: NDS = non-starchy dicotyledon seed; BGS = barley grass seed; BG = barley grain; PGS = phalaris grass seed; GS = grass seed; I = invertebrate; PT = non-seed plant tissue.**



Number of stomachs	5	6	4	6	–	26	9	8	8	3	6	7	6	8
Main food	RG	RG	GS	RG	–	RG	RG	RG	RG	RG	RG	SDS	NDS	NDS
Mean volume % of main food ±	59.2	61.1	66.1	67.6	–	64.2	91.8	98.4	98.8	79.6	98.7	57.5	75.7	39.5
standard error	24.2	19.5	19.5	16.4	–	7.0	3.0	0.8	0.6	19.9	0.4	16.3	2.7	13.6

Figure 2.7e. Breeding (A) and diet (B) of mice on rice contour banks: January to December 1979. Adult female sample sizes in brackets. Food symbols: RG = rice grain; GS = grass seed; SDS = starchy dicotyledon seed; NDS = non-starchy dicotyledon seed.



	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Number of stomachs	4	-	15	11	6	11	6	4
Main food	SG	-	SG	SG	SG	SG	SG	I
Mean volume % of main food	79.9	-	92.9	86.3	97.3	70.4	64.3	28.1
± standard error	10.6	-	1.9	3.4	1.6	7.6	10.9	11.0

Figure 2.7f. Breeding (A) and diet (B) of mice in a sorghum field: February to September 1979. Adult female sample sizes in brackets. Food symbols: SG = sorghum grain; I = invertebrate.



Figure 2.8. Milk-ripe seeds of barley grass (centre clump), and ryegrass. These weed grasses seeded prolifically on the edges of wheat and barley fields in September and October.

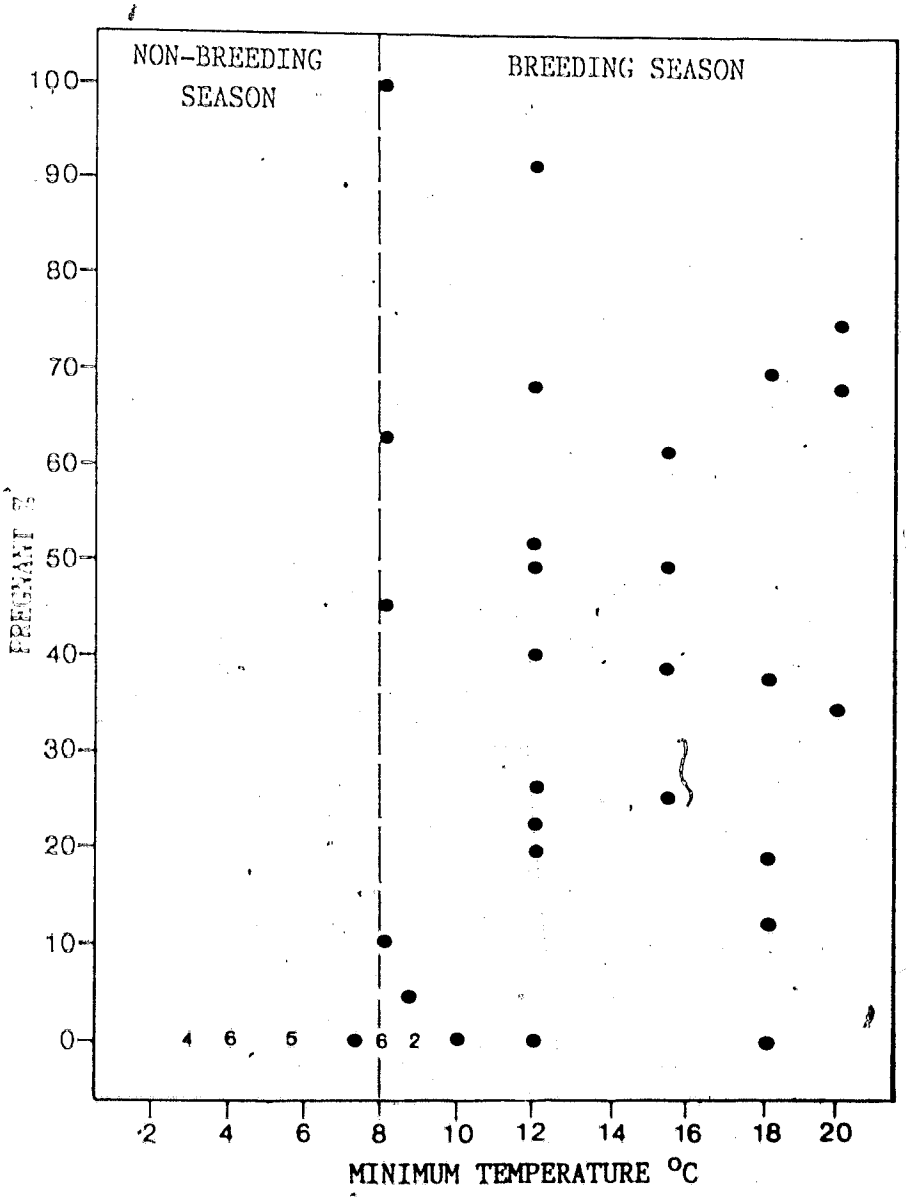


Figure 2.9. Percentage of pregnant females in the mice caught in all habitats trapped, plotted against the mean minimum temperature for the week preceding the trapping. There were no pregnancies recorded when minimum temperatures were below 8°C, but above this threshold, there was no indication of any correlation between temperature and breeding intensity. Numbers indicate superimposed points.

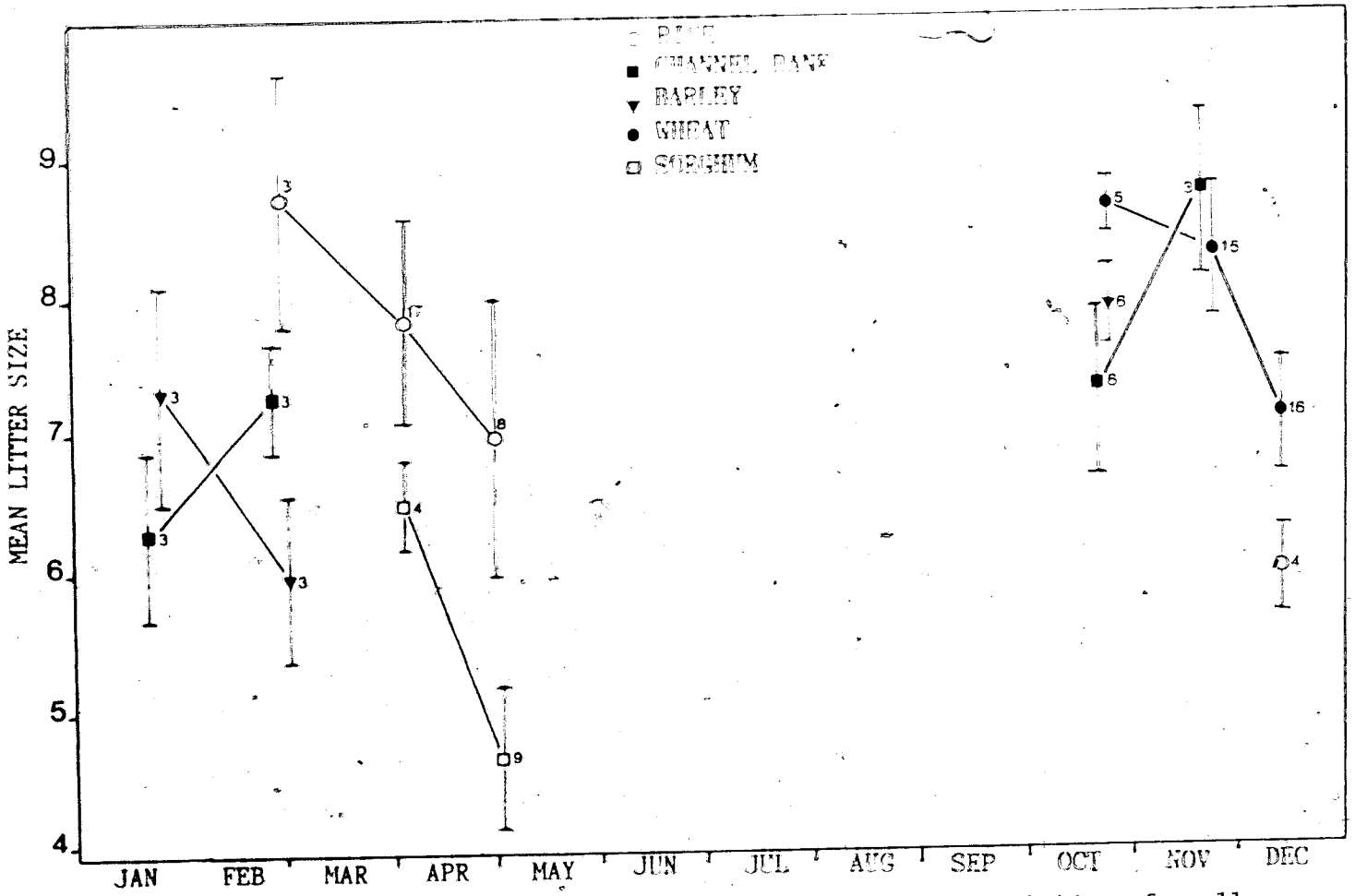


Figure 2.10. Mean litter sizes (± 1 standard error) by month and habitat for all samples ≥ three pregnant females. Samples sizes are given next to data points.

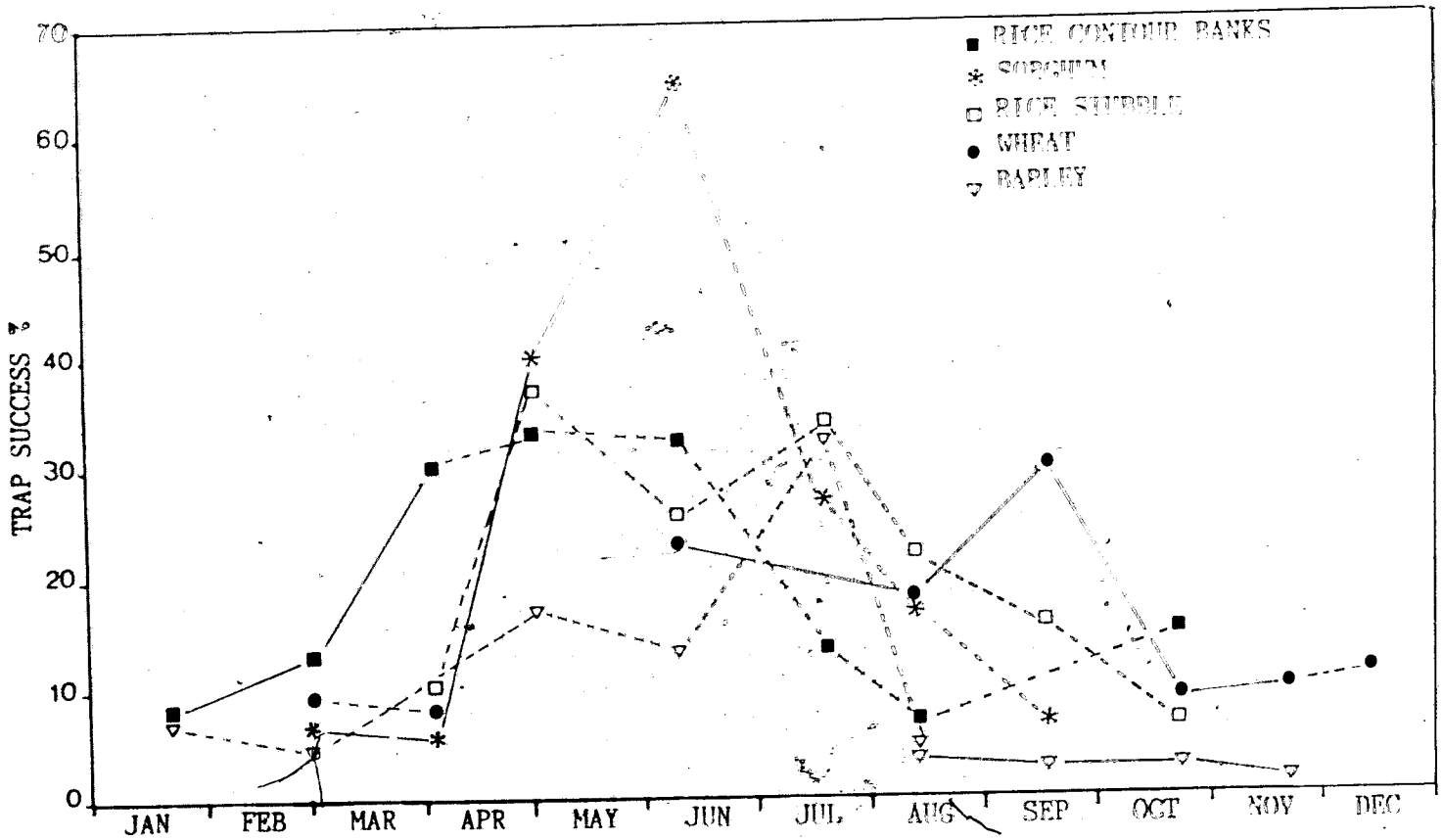


Figure 2.11. Trap success % is the average number of mice caught in 100 traps set for one night. In wheat and barley fields numbers were low in the crops in spring and summer, but increased in the barley stubble in winter to moderate levels. Mouse numbers were low in rice and sorghum crops in summer, but increased late in the breeding season and after harvest, to reach high levels, especially the sorghum stubble.

Solid lines = crop fields, broken lines = stubble fields.

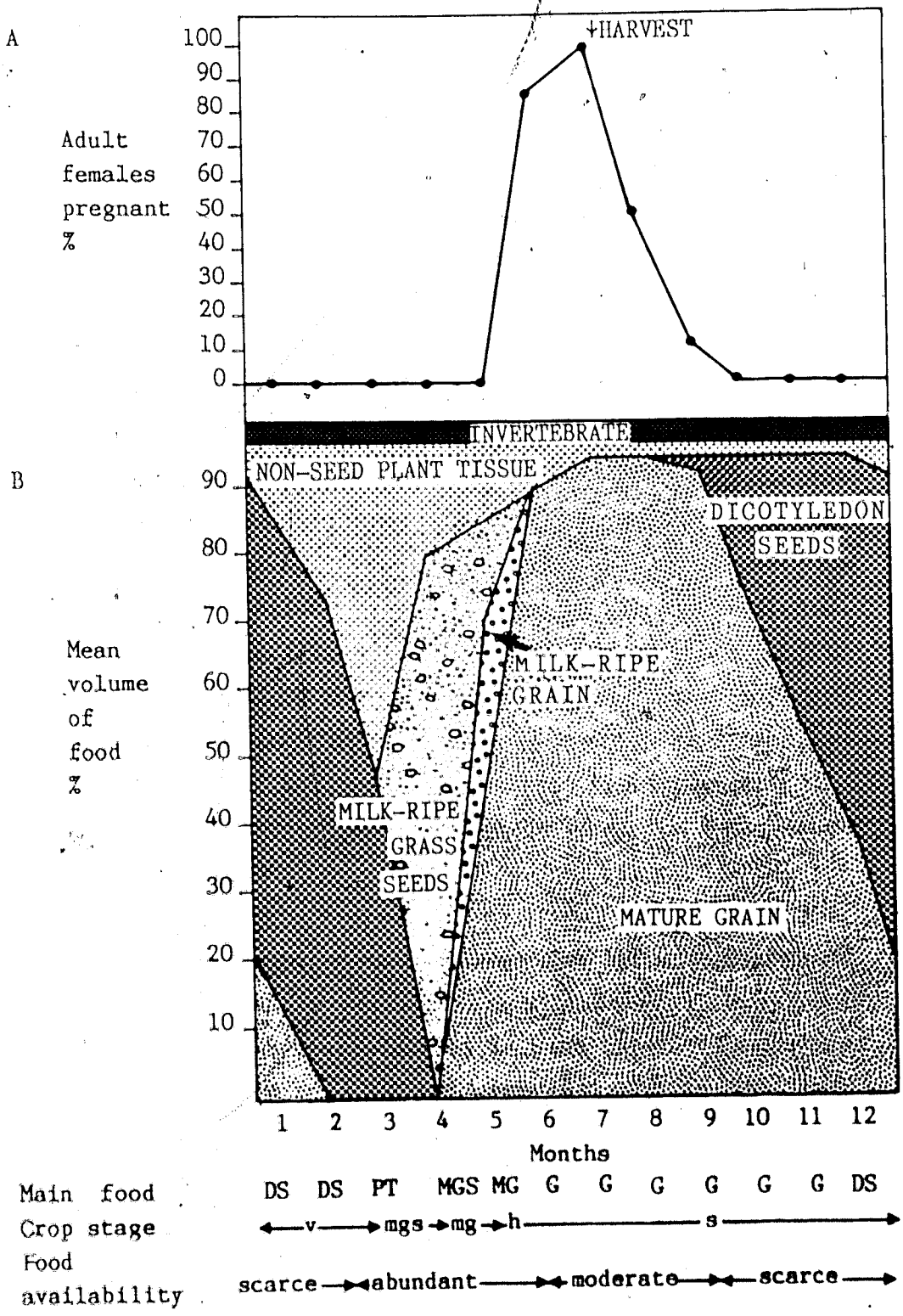


Figure 2.12. Model of changes in breeding (A) and diet (B) in relation to the stages of crop growth and harvest. Breeding can start in any month from October to March. Food symbols: PT = non-seed plant tissue; MGS = milk-ripe grass seed; G = grain; DS = dicotyledon seed. Crop stage symbols: v = vegetative; mgs = milk-ripe grass seeds; mg = milk-ripe grain; h = harvest; s = stubble.

CHAPTER THREE

A FIELD EXPERIMENT TO EXAMINE THE EFFECT OF FOOD AVAILABILITY ON THE ONSET OF BREEDING

3.1. INTRODUCTION

In Chapter Two information was reported on seasonal and habitat changes in the availability of natural foods, and corresponding changes in diet, for mice on MIR cereal farms, together with data on the timing and intensity of their breeding. As discussed earlier (Section 2.1), collection of this type of descriptive data is the first step in the investigation of the possible limitation of by food supplies. The next step is to use this information to pinpoint likely areas where food limitation of breeding may occur and to formulate hypotheses regarding the nature of these relationships. The final step is the field testing of these hypotheses.

The initial descriptive study showed that breeding recommenced after winter in different habitats at different times, and that this onset of breeding occurred in each habitat soon after grass and grain seeds ripened and were included in the diet. From these observations it was concluded that this might be one area where food limitation of breeding operates, because it appeared that food supplies might be inadequate to meet the mice's requirements for reproduction until this new food became available. This led to the formulation of the hypothesis that breeding by mice in rice fields in spring is limited by the food supplies, because they are either inadequate in 1) energy content, or in 2) quality. In the present chapter a field experiment is described which tested this hypothesis in a rice field in the spring of 1981.

The effects of food quality on breeding can be tested either by controlled laboratory experiments (Deol and Truslove 1957; Hoag and Dickie 1962; Knapka *et al.* 1977), or by less rigidly controlled field experiments. Problems with field experiments include their expense, the difficulties encountered in achieving adequate replication and sample sizes, and the high levels of variance that can be introduced by uncontrolled factors such as the age, genotype, social structure and density of the experimental populations, and the availability of natural food. Despite these problems, Snyder (1976) believes that studies on natural populations of small mammals 'need to use more widely an experimental approach in which both control and experimental groups can be free ranging populations', and further, he considers that the decrease in precision (from a laboratory or similarly controlled situation) may be more than compensated for by an increase in validity or applicability of the results. For these reasons, and because the effects of food-quality had not previously been tested in the field for house mice, it was decided that a field experiment would be the best approach for testing the hypothesis.

3.2. METHODS

3.2.1. Study-site

Selection of a study-site involved finding a rice crop that met the following specifications:

1. A two-year successional rice rotation, where a rice crop had been planted in the spring of 1980 and harvested in autumn 1981, and another rice crop was to be planted in the spring of 1981 for harvest in autumn 1982. This was to increase the liklihood that a mouse population would be well established in the field before

the start of the experiment.

2. A field with an area of at least 40 ha sown to rice, and with a sufficient number of contour banks to accommodate the treatments described in Section 3.2.2. Each contour bank needed to be at least 450 m long and 30 m from neighbouring banks along its full length. This length was required to lay out the treatments and traplines. The minimum distance between banks was chosen because Redhead (1982) found very few mice move more than 30 m between captures.

3. A field with low heterogeneity over its whole area, in terms of soil type, vegetation type or density, variety of rice grown, and mouse population density, so that variation between banks due to causes other than treatment effects would be minimal.

The rice crop on Farm 39G in the Warrawidgee district of the MIR was selected from the thirty crops inspected, as coming closest to meeting these specifications. This farm had a field of 44 ha of inga variety rice harvested in autumn 1981, and the farmer intended to re-sow this type of rice in the field in the following spring. Inspection of the field showed that it had a fairly uniform vegetation cover on its contour banks, and preliminary live-trapping at six random locations on these banks in mid-July 1981, yielded a trap success exceeding 50% at all locations. The field contained seventeen contour banks, but four came within 30 m of a neighbouring bank somewhere along their length, and so were excluded. A further four banks were shorter than the required 450 metres, but this problem was overcome by treating a pair of short banks as the equivalent of a single long bank. This meant that the field contained the functional equivalent of eleven long banks suitable for inclusion in the experiment (Figure 3.1).

On 20 September 1981, the farmer burnt the old rice stubble. The remaining vegetation was sprayed with 'Weedazol' and 'Round-up' herbicides on 10 October, and the contour banks were graded on 23 and 24 October. These treatments reduced the vegetation on the banks. The new rice crop was sown between 16 and 23 October with inga rice grain treated with DDT and fungicide. The first flush of irrigation water was applied on 22 October, the second flush on 30 October, and the permanent irrigation water on 12 November.

Random ground searches indicated that natural food supplies on the contour banks and adjacent bays were low, consisting mainly of small quantities of rice grain left on the ground from the previous crop, and the newly sown rice grain. The herbicide treatment of the field retarded the growth of spring grasses, so few fresh grass seeds became available during the experiment.

Figure 3.2 shows mean weekly temperatures and rainfall during the experiment. There was enough rain before the irrigation water was applied to prevent the soils from drying out, so mice were able to burrow and construct nests at all times.

3.2.2. Supplementary feeding

There were four experimental treatments; three types of supplementary food, and a control with no supplement. The unit for application of a treatment was a single long bank, or a pair of short banks, and the field had the equivalent of eleven such unit banks. Treatment replicates were divided among these unit banks as listed below. The allocation of treatments to particulr banks was random, and the layout of treatments on banks is shown in Figure 3.1.

Treatment 1. (2 banks) Wheat grain was provided to increase the energy content of the food supplies. The wheat grain used was grown on an MIR farm. It was coarsely broken before being fed to the mice as described below.

Treatment 2. (2 banks) Wheat grain plus GA_3 was provided to improve both the energy and quality of the food supplies, as GA_3 was thought to be a breeding stimulant (Section 2.4). Each kilogram of wheat had 100 ml of 10^{-5}M GA_3 thoroughly stirred into it, and this was spread out on trays to dry at room temperature before being used. This concentration of GA_3 was chosen so that a mouse eating between 0.5 g and 5.0 g of treated wheat per day, would have a consumption of GA_3 in the range found by Olsen (1981) to stimulate reproduction (Section 2.4). The wheat was coarsely broken in a cleaned soil grinder to expose the endosperm before being treated with the GA_3 solution, because preliminary observations on caged mice showed they were inclined to eat the wheat endosperm but leave most of the seed coat uneaten. To ensure that the wheat fed to mice for Treatment 1 would act as a valid control treatment for the effects of GA_3, all wheat used in Treatment 1 was also coarsely broken, but instead of being mixed with GA_3 solution, it was mixed with distilled water.

Treatment 3. (3 banks) Commercial mouse pellets were provided to improve both the energy and nutrient quality of the food supplies. The pellets used were Fidelity Feeds rat and mouse cubes, which were formulated to provide all the nutrients required by caged mice for intensive breeding. The analysis of their nutrient content is given in Appendix 1. Later experiments showed mice from the MIR bred well in the laboratory when fed these pellets (Section 4.3).

Treatment 4. (4 banks) No supplementary food was provided for the control treatment.

On 15 September a single row of 50 feeders was put out on each long bank, or two rows of 26 feeders on paired short banks. Feeders were placed at 8 m intervals along the banks. Each feeder was a 15 cm length of PVC pipe, 5 cm in diameter, which was partly closed off at each end with a small piece of sheet steel, to hold in the food (Figure 3.3). These were similar to the feeders used by Redhead (1982) and mice readily entered and fed from them. Feeders were checked daily for the duration of the experiment and food that was wet or eaten was replaced. Food was always provided in excess of removal rates.

On the nights of 16 and 17 October, mid-way between trap-sessions T2 and T3, the weight of food removed from each feeder was recorded. The food was weighed before being placed in the feeders, and after the two nights all remaining food was collected, dried, separated from faeces or other debris, and weighed.

After the final live trap-session in November, snap-traps were laid along all experimental banks for two nights to catch mice for analysis of stomach contents. Snap-traps have about one-tenth the trap-success rate of Longworth traps (Redhead and Bomford, unpublished data). The population density was very low by this time and only one mouse was caught. Therefore the diet of mice under the different treatments was not determined.

3.2.3. Population monitoring

The mouse population was live-trapped before the experimen-

tal treatments started (pre-treatment trap-session T1, 5 - 13 Sept.), and during the treatments (treatment trap-sessions T2, 6 - 12 Oct.; T3, 20 - 26 Oct.; T4, 27 Oct. - 2 Nov.; T5, 14 - 20 Nov.). Feeders were left in place and kept filled with food on trap-nights. In each trap-session, the eleven banks were trapped for three successive nights with Longworth traps baited with wheat grain. As insufficient traps were available to trap all banks simultaneously, the banks north of the track shown on Figure 3.1 were trapped on the first three nights, followed by the banks to the south. Traps were removed from the banks on nights when there was no trapping. On long banks (50 feeders) there were two rows of twenty traps, with the three feeder sites at each end and the four centre feeder sites left vacant. On short banks (26 feeders) there were single rows of twenty traps, with three feeder sites left vacant at each end. Single traps were set within a metre of feeder sites.

The captured mice were removed from traps in the morning. Their weight was measured to the nearest 0.1 g by suspending them by the tail from an alligator clip on a Pesola spring balance. Head + body length, from anus to snout tip, was measured to the nearest millimetre by gently stretching each mouse on its back along a ruler. Testes were scored as 'scrotal' if they were in the scrotal sac or could easily be moved into it; otherwise as 'abdominal'. Vaginae were scored as 'open', 'closed but perforate', or as 'imperforate' if they were sealed by a membrane. Females were scored as 'pregnant' if embryos could be felt by abdominal palpation, and as 'lactating' if milk could be expressed from their nipples. Only pregnant or lactating females were scored as 'breeding', and as only females with a head + body length ≥80 mm were ever found to be breeding in this experiment, only females of this length were classified as adults. All captured mice were tagged with Hauptner minature ear tags which were stamped with a four digit number for individual recognition,

before [redacted] released at the site of capture. In the final trap-sessi[redacted] mice were killed and frozen for subsequent body-fat [redacted]lysis.

As an addition to the main experiment, three trap-sessions were also conducted in a neighbouring wheat crop, in the intervals between the rice field trap-sessions. This habitat had an abundant supply of high-quality food at this time, and the trapping was conducted to determine if breeding commenced earlier in this habitat than in the rice field habitat, as had happened in spring 1979 (Figure 2.7c,e). Four rows of traps were set in each trap-session, each of forty traps spaced at 8 m intervals along a contour bank. Each contour bank was at least 30 m from its nearest neighbour along its entire length, and in each trap-session traps were set for three successive nights.

3.2.4. Data analysis

The data unit was the number of mice caught per bank in each trap-session (n), or subsets of this unit. As a uniform trapping effort was made in each trap-session (120 trap-nights per bank per trap-session) the data for the number of mice caught on each bank in each trap-session was taken as an index of the number of mice present on each bank. As the trap-success never exceeded 50% on any bank, and was mostly closer to 10%, no corrections factors were introduced for trap-saturation. Data for T1, the pre-treatment trap session, was analysed in the same manner as data for later treatment trap-sessions. As experimental treatments had not started in T1, these analyses were conducted on data for mice destined to receive the different treatments. This was to test if there were any initial differences between the bank populations before the treatments started

The analysis was restricted to between treatments within trap-sessions. No analyses were conducted between trap-sessions because data sets from trap-sessions were not independent of each other, as the same banks were re-trapped in each trap-session, and recaptured mice were included in the samples. This meant data from trap-sessions separated by small time intervals would have been more closely correlated than data from more widely spaced trap-sessions. Data for the following parameters was analysed for treatment effects:

1. n = Total mice
2. f = Adult females
3. m = Mice recaptured from previous trap sessions
4. h = Adult females recaptured from previous trap sessions
5. W = Weights of males
6. L = Lengths of males

7. $F = \frac{\text{number of adult females caught on banks (f)}}{\text{total number of mice caught on banks (n)}}$

8. $T = \frac{\text{number of recaptured mice caught on banks (m)}}{\text{total number of mice caught on banks (n)}}$

9. $P = \frac{\text{number of recaptured females caught on banks (h)}}{\text{number of adult females caught on banks (f)}}$

10. $B = \frac{\text{number of breeding females caught on banks (r)}}{\text{number of adult females of females caught on banks (f)}}$

Data for parameters 1 to 4, were tested for treatment effects by one-way anaysis of variance. Data on parameters 6 and 7 were used to calculate condition indexes, and these were analysed for treatment effects by testing the regression lines of $\log_e$ weight on $\log_e$ length for difference in slope or intercept. Data on proportions, parameters 8 to 10, were analysed by logistic regression. To test whether the quality of the food affected any

of these parameters, data sets for Treatments 1 (wheat), 2 (wheat-GA_3), and 3 (pellets) were tested against each other for treatment effects. To determine whether the provision of supplementary food affected these parameters, data sets for Treatments 1, 2, and 3 were combined as a Feeding Treatment and tested against the data set for Control Treatment 4. A brief outline of the three types of analysis follows.

i) Analysis of variance tests. Sources of variation and associated degrees of freedom used in one-way analysis of variance tests are presented in Table 3.1. Regression models for which a normal distribution of errors was assumed, were found to give the best fit to data sets on numbers of mice, so all analyses were conducted on untransformed data. Calculations were facilitated by use of the program GENSTAT (Alvey *et al*, 1977). Variance ratios were checked against percentiles of the F distribution to determine if there were any significant treatment effects. In all analysis of variance tests, residuals were plotted against fitted values to check for outliers. None were detected and all analyses were conducted on complete data sets. An example of this type of analysis is presented in Appendix 2c.

ii) Logistic regression. This method of analysis tested for treatment effects by fitting generalized linear models to the data using the logit link function, and assuming a binomial distribution of errors, and then calculating the deviance associated with each model (McCullagh and Nelder 1983). This analysis was also facilitated by use of the program GENSTAT. This method of analysis was designed for this type of binomial data, and hence was thought to be more reliable than a traditional analysis of variance on arc-sine transformed data, because the assumptions that had to be made for the use of logistic regression analysis were more likely to be met than those that are made for an analysis of variance. Also, logistic regression takes

into account differences in sample size, which are considerable in the data sets for the present experiment, whereas this information is ignored when arc-sine transformations are made. The general principles of logistic regression as it was used are described below, and an example of an analysis is presented in Appendix 2d.

If the probability that a mouse will breed after being fed foods 'i' and 'j' is θ_{ij} = P(breed), then as θ_{ij} is a probability, it must take values $0 \leq \theta_{ij} \leq 1$, and in logistic regression θ_{ij} is defined as follows:

$$\theta_{ij} = e^{LMij}/(1 + e^{LMij})$$

where LMij is any linear model which contains parameters (of unknown value) to describe the systematic part of the data variation. The odds ratio, P(breed)/P(not breed), is therefore:

$$\theta_{ij}/(1 - \theta_{ij}) = e^{LMij}$$

and the log odds ratio, Λ_{ij}, is:

$$\Lambda_{ij} = \ln e^{LMij} = LM_{ij}$$

An example is:

$$\Lambda_{ij} = \mu + \alpha_i + \beta_j + \gamma_{ij}$$

where μ is a constant, α_i is a parameter which describes the effect of food 'i', β_j describes the effect of food 'j' and γ_{ij} describes the effect of the interaction between foods 'i' and 'j'.

In logistic regression, θ_{ij} is estimated by $\hat{\theta}_{ij}$:

$$\hat{\theta}_{ij} = r_{ij}/f_{ij}$$

(r = number of females that breed, f = total number of females)

and Λ_{ij} is estimated by λ_{ij}:

$$\lambda_{ij} = \ln(\hat{\theta}_{ij}/1 - \hat{\theta}_{ij})$$

$$= LM_{ij} + \varepsilon_{ij}$$

where ε_{ij} is the term representing the random part of the data variation not accounted for by the parameters in the LM_{ij}. An example is:

$$\lambda_{ij} = \mu + \alpha_i + \beta_j + \gamma_{ij} + \varepsilon_{ij}$$

Maximum liklihood estimates of the parameters μ, α_i, β_j and γ_{ij} are found by use of an iterative least squares algorithm. These fitted parameter values can then be used to calculate $\hat{\lambda}_{ij}$:

$$\hat{\lambda}_{ij} = \mu + \alpha_i + \beta_j + \gamma_{ij} \qquad \text{Model 1}$$

This $\hat{\lambda}_{ij}$ can then be used to calculate $\hat{r}_{ij}$:

$$\hat{r}_{ij} = f_{ij}(e^{\hat{\lambda}ij}/(1 + e^{\hat{\lambda}ij}))$$

Model 1 is a full model, containing parameters for all sources of systematic variation. Other models, with one or more of these parameters omitted may also be fitted. A quantity known as the Deviance (DV), with associated degrees of freedom (d.f.), is calculated for each model:

$$DV = 2[\sum r_{ij}\ln(r_{ij}/\hat{r}_{ij}) + \sum(f_{ij} - r_{ij})\ln(\frac{(f_{ij} - r_{ij})}{(f_{ij} - \hat{r}_{ij})})]$$

This DV value is approximately distributed as a χ^2 variate. The data is assumed to have a true binomial distribution, and this means that the value of DV/d.f. approaches 1.000 when the model fits the data well (ie. the scale parameter is set at 1.000).

The DV can be considered as analogous to the residual sum of squares in ordinary analysis of variance or regression models. The significance of the different can be tested by fitting successive models, each with a parameter set that is a subset of the previous model fitted. When a full model is fitted the DV is of course zero, but the DV increases as parameters are omitted from the model. The difference in DV between two such models approximates a χ^2, with associated d.f. also obtained from the difference in d.f. of the two models. For example:

Model 1 = $\mu + \alpha_i + \beta_j + \gamma_{ij}$ $DV_1 = 0$, $d.f._1 = 0$ full model

Model 2 = $\mu + \alpha_i + \beta_j$ $DV_2 = x$, $d.f._2 = a$

Model 1 - Model 2 = γ_{ij} $DV_2 - DV_1 = x$, $d.f._2 - d.f._1 = a$

The difference in deviance value 'x' with 'a' d.f. will give an estimate of the significance of the parameter γ_{ij} when tables of χ^2, are consulted. Difference in deviance values for parameters α_i and β_j can be calculated by the same method.

iii) Condition indices. Redhead (1982) calculated a condition index for each mouse as follows. For each sample of mice he regressed $\log_e$ weight (ln W) on $\log_e$ length (ln L). He calculated the mean value of ln L for all mice in all samples to be 4.3584. The ln W corresponding to a ln L of 4.3584, was taken as a measure of condition index. He tested regression lines for 76 samples of mice for differences in slope. When samples had slopes that were not significantly different, he grouped them together, and this gave two groups. Only for samples in the same group, did he compare condition indices.

In the present study, data for body weights and lengths for males from feeding banks were compared to that for males from control banks for each trap-session. Values for '$\log_e$ weight' were regressed on '$\log_e$ length' and the regression line for males from feeding banks was compared to the line for males from control banks for differences in slope or intercept. This analysis was facilitated by use of the PARALLEL macro in the package GENSTAT, following Redhead (1982). Data for females were not analysed because the presence of pregnant and lactating individuals in the samples would have prevented a meaningful interpretation.

3.3. DESCRIPTION OF POPULATIONS

The demography of populations may affect breeding performance, so information on total numbers, numbers of adult females, and recapture rates, together with the results of tests on these parameters for treatment effects, are presented in this section.

3.3.1. Total numbers

The total numbers of mice caught on banks in each trap-session (n) are presented in Table 3.2a. Initially, the numbers of mice on all banks were moderately high, with an average catch of $n = 38 \pm 5$ (one S.E.) per bank in the pre-treatment trap-session T1. But trap success declined rapidly in later trap-sessions on both feeding and control banks.

Data for total numbers of mice were analysed for treatment effects and the results of these tests are presented in Table 3.2b. When the three supplementary feeding treatments were com-

pared, a significant treatment effect was only found in T5, when wheat treatment banks had significantly more mice than the other feeding treatment banks ($p<0.05$). It was concluded that this experiment did not produce evidence for a food-quality effect on numbers, as the occurrence of an isolated statistically significant effect of one food in one trap-session was considered to be minor evidence to the contrary. When the three feeding treatments were lumped for an analysis of feeding (7 banks) versus control (4 banks) treatments, a highly significant effect was found in trap-session T3 ($p<0.001$), but there were no significant differences in any other trap-sessions. This single significant result possibly indicates that the decline in numbers that occurred on all banks was slightly delayed by supplementary feeding, but even if this interpretation is correct, the delay was only of short duration, as by the last trap-session, there were slightly more mice being caught on control banks than on feeding banks.

3.3.2. Numbers of adult females

The data for the numbers of adult females (f) are presented in Table 3.3a. This parameter is of interest because it determines the reproductive potential of the populations. A decline in adult female numbers occurred over the experimental period on all banks. These data were analysed for treatment effects (Table 3.3b). No treatment effects due to food-quality were found, and a treatment effect due to feeding was only found in T3 ($p<0.05$). These analyses were conducted on small sample sizes, and so any treatment effect might easily have been masked by random variation. As a solution to this problem data sets were pooled as follows. Data from T2 and T3 were combined to form a data set T23, and data from T4 and T5 were likewise combined to form T45. Any individual female present in both data sets to be combined, was only counted once. These pooled data sets are presented in

Table 3.4a, and the results of their analysis for treatment effects in Table 3.4b. Once again, food quality showed no treatment effects, but supplementary feeding had a significant effect in both T23 ($p<0.05$) and T45 ($p<0.05$), with higher female numbers on feeding banks.

Data for fitted mean values for the proportion of adult females in the total catch (f/n) are presented in Table 3.5a, together with fitted mean values for these proportions ($F\% = 100\Sigma f/\Sigma n$) The results of the analyses of these data for treatment effects are presented in Table 3.5b. There was no treatment effect due to food quality in any trap-session, and only in T3 was there a significant treatment effect due to supplementary feeding ($p<0.05$). Once again data from successive trap-sessions was pooled to increase sample sizes for this parameter, and these pooled data are presented in Table 3.6a, and the results of their analysis in 3.6b. No significant treatment effects were found in these pooled data.

3.3.3. Recaptures

Data for the number of recaptures from previous trap-sessions (m) are presented in Table 3.8a. Sample sizes of recaptured mice were too small to allow a meaningful analysis of treatment effects on on-site survival rates. But data for the proportion of recaptured mice (m/n) are also presented in Table 3.8a, together with fitted mean proportions ($T\% = 100\Sigma/\Sigma n$), and these T% values indicate the proportion of known residents in the bank populations. On control banks there was a decline in each successive trap-session in the proportion of recaptured mice. On feeding banks, in contrast, there was an increase in the proportion of recaptured mice in each successive trap-session, until the final trap-session T5, when the proportion of recaptures

dropped. The results of the analysis of these data for treatment effects are presented in Table 3.8b. There was only a significant treatment effect due to food quality in T2, when there was a significantly higher proportion of recaptures on the wheat treatment banks than on the banks with other feeding treatments ($p<0.05$). There was a significant treatment effect due to supplementary feeding in T4 ($p<0.05$) and T5 ($p<0.01$), when feeding banks had a higher proportion of recaptures than control banks. These data suggest that supplementary feeding increased the proportion of residents in the bank populations.

Data for the proportion of adult females that were recaptures (h/f) are presented in Table 3.9a, together with fitted mean proportions ($P\% = 100\Sigma h/\Sigma f$). The proportion of adult females recaptures increased in successive trap-sessions on feeding banks but was uniformly low on control banks, and in trap-sessions T3 and T4 there were no adult female recaptures, and only a single one in T5. The results of the analysis of these data are presented in Table 3.9b. There were no treatment effects due to food quality in any trap-session. There were significant effects due to supplementary feeding in T3 ($p<0.05$), T4 ($p<0.01$), and T5 ($p<0.05$). These results suggest that the proportion of resident females was high on feeding banks, but that the females caught on control banks were probably short-term residents or transients.

3.3.4. Movements

There were few records of movements of mice between experimental banks. Of the 42 female mice that were recaptured one or more times, none had changed banks. Of the 48 males recaptured one or more times, only four (8.3%) had changed banks. Two males moved from control to feeding banks, one from a feeding bank to a

control bank, and one from a feeding bank to another feeding bank. These data suggest there was no general movement of mice from control banks to feeding banks.

3.4. RESULTS

3.4.1. Amounts of food supplement eaten

The measurements of the mean dry weights of food removed from feeders on the combined two nights of 16 and 17 October were 13.2 ± 0.6 (one standard error) for the grain feeders, and 12.4 ± 1.4 g for the pellet feeders. Seventy-eight per cent of all feeders had at least 4 g of food removed from them. The 22% that had less than 4 g removed were evenly distributed between banks and between treatments. Birds and ants were rarely observed visiting the feeders, and it was thought that nearly all food removal was due to mice.

No other measurements were made on food removal rates, but there was an obvious decline in removal rates over the nine week duration of the feeding treatment, which coincided with the decline in mouse numbers.

3.4.2. Breeding intensity

Only females that were pregnant or lactating were classified as breeding, and the proportion of adult females that were breeding (r/f) was taken as an index of breeding intensity (B) and was usually expressed as a percentage ($B\% = 100\ \Sigma r/\Sigma f$).

Burrows were often constructed right next to feeders, and food from these feeders could be observed in the burrow entrances

(Figure 3.4). Traps set at these feeder sites often caught breeding females. The data for numbers of breeding females (r), together with the total numbers of adult females (f), and fitted values for breeding intensity (B%) are presented in Table 3.9a. Some mice were found to be breeding in the preliminary trapping conducted in mid-July (B% = 19.6%), and in the pre-treatment trap-session (T1) conducted in the second week of September, when the mean B% of the eleven banks combined was 18.7%. These findings suggest that breeding probably continued through the winter in this rice stubble field in 1981. In the four treatment trap-sessions (T2 to T5) no breeding females were caught on any of the control banks, but on the feeding banks breeding intensity increased after the feeding treatments started, and remained between 30% and 60% in trap-sessions T2 to T5 (Figure 3.5).

The results of the analysis of the data for breeding intensity are presented in Table 3.9b. There were no treatment effects due to food quality in any trap-session. There were significant treatment effects due to supplementary feeding in T3 ($p<0.05$) and T4 ($p<0.01$).

As described above (Section 3.3.2), sample sizes in these adult female data sets were small, so data from successive trap-sessions were again pooled by the above method to increase sample sizes. Any individual female listed in both data sets was only counted once, and if she was scored as breeding in either data set she was scored as breeding in the pooled set. The combined data sets T23 and T45 for breeding intensity are presented in Table 3.10a, and the results of their analysis for treatment effects in Table 3.10b. Once again there were no treatment effects due to food quality. There were highly significant treatment effects due to supplementary feeding in both T23 ($p<0.01$) and T45 ($p<0.01$), with a higher proportion of breeding females on feeding banks than on control banks.

The data for the three trap-sessions conducted in the wheat field, on numbers of females and the proportion breeding, are presented in Table 3.12. This data is also included in Figure 3.5. Although sample sizes were small, these data indicate that the breeding intensity in the wheat field increased in spring in a pattern similar to that in the wheat field in 1979 (Figure 2.7c), and also similar to that on the feeding banks in the rice field in the present experiment.

All males ≥ 80mm head-body length caught on all banks in all trap-sessions had scrotal testes. This suggested that the adult male population remained in breeding condition for the duration of the experiment.

3.4.3. Condition indices

The body condition of males from feeding banks was compared to that of males from control banks. Values of $\log_e$ weight (ln W) were regressed on values of $\log_e$ length (ln L) and the feeding and control regression lines were tested for differences in slope or intercept. The results of this analysis are presented in Table 3.12. A significant differences in slope and intercept was found only in T3. This showed that feeding the supplements did not affect the weight-length relationship in any other trap-session. For the T3 data, the confidence intervals around the fitted value for ln W were calculated for the minimum, mean and maximum values of ln L. The confidence intervals around the feeding and control values of ln W showed considerable overlap for all three ln L values, so it was concluded that over the range of body lengths in these samples, the feeding treatment did not affect the weight-length relationship.

3.4.4. Body fat

Males caught in the final trap-session that were recaptures from previous trap-sessions, were analysed for body-fat content by the method previously described (Section 2.2.7). Recaptured mice were selected, as they had probably been exposed to the feeding treatments for the longest time. There were insufficient bodies to compare the effects of the three different feeding treatments, but enough to compare mice from feeding banks to those from control banks. The mean body fat (± one standard error) of males from fed banks was 17.4±0.7% (n = 13), and from control banks was 18.2±1.7% (n = 13). There was clearly no treatment effect on the body-fat content of these mice. Females were not analysed because the presence of pregnant and lactating mice in the samples would have prevented a meaningful interpretation of these data.

3.5. DISCUSSION

Breeding on banks with supplementary food was continuous from late winter through spring, in contrast to breeding on control banks, which ceased in early spring. As this difference in breeding intensity is statistically significant, the null hypothesis, that breeding intensity in spring is not affected by food supply, is rejected.

On banks with supplementary food, adult females were present in higher densities, and remained resident longer, than on control banks. Therefore, not only was breeding intensity higher on feeding banks, but more females were present to breed.

While it was clearly shown that breeding was food limited, there was no indication that the different food qualities affect-

ed breeding performance. But the data showed a high within-treatment variance, and this could have masked treatment effects. Therefore, the hypothesis that food quality was limiting for breeding could be neither accepted nor rejected. The high within-treatment variance was probably caused by both variation in the amount of natural food available, and by the small sample sizes of mice. The first factor is probably beyond experimental control, but the second factor could be compensated for, in a future experiment, by increasing the number of treatment replicates, or alternatively, by conducting the experiment in a year when mouse numbers were higher than in the present experiment. An alternative approach would be to conduct experiments on caged mice kept under controlled laboratory conditions.

The results of this experiment support Bronson's (1979) suggestion that seasonal breeding reflects seasonal changes in food availability. They also support the suggestion made in Chapter Two, that the asynchronous onset of breeding in different fields, reflects the different times when food becomes available.

Supplementary food failed to affect body fat contents. Reproductively active house mice usually have a lower body fat content than non-breeding mice (Redhead 1982). Therefore the continuous breeding of mice on feeding banks may have prevented the extra energy made available by the supplementary food from being deposited as body fat. The weight-length relationship was also not affected by the supplementary food, and this suggests that Redhead's condition index may be determined by factors other than food supply. Pryor and Bronson (1981) did not find that body weights were affected by food quality, in their laboratory studies on wild-strain mice.

Mouse numbers usually decline in rice fields in winter and early spring (Figure 2.11; Redhead 1982). If this decline is

caused by food shortage, then the provision of supplementary food should prevent it. In the present experiment, supplementary food did not prevent a decline in population density. Therefore the decline must have been caused by some factor other than food shortage. As the vegetation cover was poor on most of the experimental banks after the farmer burnt the old stubble, predation may have contributed to the decline, as there were many potential predators. Newsome *et al.* (1976) found predators caused the population density of a wild house mouse population in California to decline, even when supplementary food and water was provided. DeLong (1967) and Redhead (1982) also found supplementary feeding did not prevent population declines, and they attributed the decline in density they observed mainly to social factors. Redhead thinks the spacing behaviour of mice in breeding condition is more effective than that of non-breeding mice. If this is true, mice whose breeding intensity has been increased by the provision of supplementary food, would not be expected to have a higher density than mice with no extra food, but rather, to show more territorial activity and longer residency times. There was some suggestion of longer residency times in the present study, so these data support Redhead's theory. Hence although good food supplies may increase breeding intensity and the duration of the breeding season, they do not necessarily cause numbers to increase to plague-like densities. Only Newsome (1970) found supplementary food prevented a decline in numbers, but why his results differed from the others is not yet clear.

A comparison of the results and conclusions presented in this chapter, with supplementary feeding experiments conducted in other studies, is deferred to Chapter Six.

Table 3.1. Sources of variation and degrees of freedom used in analysis of variance tests for treatment effects on numbers of mice caught

Source	Degrees of freedom
Pellets v wheat v GA3-wheat	2
Feeding v control	1
Residual	7
Total	10

Table 3.2a. Numbers of mice caught (n) and treatment means ($n_{treatment}$)

Trap session	Pellets three banks			$n_{(p)}$	Wheat two banks		$n_{(w)}$	GA_3-wheat two banks		$n_{(ga)}$	$n_{(feed)}$	Control four banks				$n_{(c)}$
T1	46	47	48	47	65	11	38	34	52	43	43	39	25	34	19	29
T2	39	13	16	23	16	11	14	23	15	19	19	12	11	8	4	9
T3	20	24	14	19	10	11	11	21	13	17	16	4	11	4	2	5
T4	11	8	12	10	6	7	7	8	12	10	9	4	8	4	8	6
T5	5	10	4	6	17	14	16	7	9	8	9	13	10	13	6	11

Table 3.2b. Variance ratios from analysis of variance tests for treatment effects on the numbers of mice caught (n)

	Treatment	
Trap session	Pellets v wheat v GA_3-wheat $F_{(2,7)}$	Feeding v control $F_{(1,7)}$
T1	0.183	1.884
T2	0.723	3.837
T3	2.587	16.274***
T4	2.078	5.307
T5	6.198*	0.340

* $p<0.05$,
*** $p<0.001$
For method see Appendix 2c.

Table 3.3a. Numbers of adult females caught on banks (f) in each trap-session, and treatment means ($f_{treatment}$).

Trap session	Pellets three banks			$f_{(p)}$	Wheat two banks		$f_{(w)}$	GA_3-wheat two banks		$f_{(ga)}$	$f_{(feed)}$	Control four banks				$f_{(c)}$
T1	20	13	12	15	19	1	10	19	13	16	14	19	7	10	6	11
T2	10	2	3	5	1	4	3	5	3	4	4	2	2	0	1	1
T3	10	10	2	7	4	4	4	6	5	6	6	0	2	1	0	1
T4	4	4	3	4	2	0	1	3	3	3	3	1	0	1	3	1
T5	1	4	1	2	3	2	3	1	2	2	2	1	2	1	0	1

Table 3.3b. Variance ratios from analysis of variance tests for treatment effects on the numbers of adult females caught (f)

Trap session	Treatment	
	Pellets v wheat v GA_3-wheat $F_{(2,7)}$	Feed v control $F_{(1,7)}$
T1	0.464	0.622
T2	0.556	2.852
T3	1.044	10.122*
T4	4.135	5.151
T5	0.389	1.980

* $p<0.05$
For method see Appendix 2c.

Table 3.4a. Pooled numbers of adult female (f) and treatment means ($f_{treatment}$).

Trap session	Pellets three banks			$f_{(p)}$	Wheat two banks		$f_{(w)}$	GA_3-wheat two banks		$f_{(ga)}$	$f_{(feed)}$	Control four banks				$f_{(c)}$
T23	19	12	4	12	5	7	6	10	5	8	9	2	4	1	1	2
T45	4	6	4	5	4	2	3	4	4	4	4	2	2	2	3	2

Table 3.4b. Variance ratios from analysis of variance tests for treatment effects on pooled data for the number of adult females (f).

	Treatment	
	Pellets v wheat v GA_3-wheat	Feed v control
Trap session	$F_{(2,7)}$	$F_{(1,7)}$
T23	1.148	6.292*
T45	2.154	10.074*

* $p < 0.05$
For method see Appendix 2c.

Table 3.5a. Fitted mean percentage values for the proportion of adult females in mice caught (F% = 100Σf/Σn).

Trap Session	F%(pellets)	F%(wheat)	F%(GA3)	F%(feed)	F%(control)
T1	32	26	37	32	36
T2	22	19	20	21	14
T3	38	38	32	36	14
T4	35	15	30	30	21
T5	32	16	19	21	10

Table 3.5b. Differences in deviance from logistic regression analysis tests for treatment effects on the proportion of adult females in mice caught (f/n).

	Treatment	
	Pellets v wheat v GA_3-wheat	Feed v control
Trap session	X^2_2	X^2_1
T1	1.22	0.57
T2	0.149	0.852
T3	0.328	4.39*
T4	1.92	0.72
T5	1.68	2.69

* $p<0.05$

For method see Appendix 2d.

Table 3.6a Pooled numbers of adult females (f), pooled total numbers of mice (n), and fitted mean percentage values (F%) for the proportion of females in mice caught $F\%_{(treatment)} = 100\Sigma f_{(treatment)}/\Sigma n_{(treatment)}$

Trap session		Pellets three banks			F%(p)	Wheat two banks		F%(w)	GA_3-wheat two banks		F%(ga)	F%(feed)	Control four banks				F%(c)
T23	f	19	12	4	29%	5	7	26%	10	5	22%	23%	2	4	1	1	15%
	n	55	36	29		26	21		41	26			15	20	12	6	
T45	f	4	6	4	30%	4	2	14%	4	4	24%	22%	2	2	2	3	14%
	n	16	15	16		23	21		15	19			17	18	17	14	

Table 3.6b. Differences in deviance from logistic regression analysis tests for treatment effects on the pooled data sets for the proportion of adult females in the mice caught (f/n).

	Treatment	
	Pellets v wheat v GA_3-wheat	Feed v control
	X^2_2	X^2_1
T23	1.055	3.673
T45	3.579	2.221

For method see Appendix 2d.

Table 3.7a. Numbers of recaptures (m), total mouse numbers (n) and fitted mean percentage values for the proportion of recaptures in the mice caught ($T\%_{(treatment)} = 100\Sigma m_{(treatment)}/\Sigma n_{(treatment)}$)

Trap session		Pellets three banks			$T\%_{(p)}$	Wheat two banks		$T\%_{(w)}$	GA_3-wheat two tanks		$T\%_{(ga)}$	$T\%_{(feed)}$	Control four banks				$T\%_{(c)}$
T2	m	10	6	5	31%	9	6	56%	3	5	21%	33%	5	6	2	0	37%
	n	39	13	16		16	11		23	15			12	11	8	4	
T3	m	7	11	4	38%	6	5	52%	7	6	38%	46%	1	4	1	1	33%
	n	20	24	14		10	11		21	13			4	11	4	2	
T4	m	8	4	5	55%	6	3	69%	5	5	50%	56%	2	4	0	1	29%
	n	11	8	12		6	7		8	12			4	8	4	8	
T5	m	2	6	2	53%	6	2	26%	1	3	25%	33%	1	3	0	0	10%
	n	5	10	4		17	14		7	9			13	10	13	6	

Table 3.7b. Differences in deviance from logistic regression analysis tests for treatment effects on the proportion of recaptures in mice caught (m/n).

	Treatment	
Trap Session	pellets v wheat v GA_3-wheat X^2_2	feed v control X^2_1
T2	8.57*	0.20
T3	1.44	0.41
T4	1.26	5.26*
T5	4.34	8.78**

* $p<0.05$
** $p<0.01$
For method see Appendix 2d.

Table 3.8a. Numbers of recaptured adult females (h), numbers of adult females (f), and fitted mean percentage values for the proportion of adult females that were recaptures ($P\%_{(treatment)} = 100\Sigma h_{(treatment)} / \Sigma f_{(treatment)}$)

Trap session		Pellets three banks	$P\%_{(p)}$	Wheat two banks	$P\%_{(w)}$	GA_3-wheat two banks	$P\%_{(ga)}$	$P\%_{(feed)}$	Control four banks	$P\%_{(c)}$
T2	h	4 2 2	53%	1 3	80%	1 1	25%	48%	2 1 0 0	60%
	f	10 2 3		1 4		5 3			2 2 0 1	
T3	h	3 6 1	45%	2 4	50%	4 3	64%	56%	0 0 0 0	0%
	f	10 10 2		4 4		6 5			0 2 1 0	
T4	h	4 2 2	73%	2 0	100%	3 1	67%	73%	0 0 0 0	0%
	f	4 4 3		2 0		3 3			1 0 1 3	
T5	h	1 3 1	83%	3 1	80%	0 2	67%	73%	0 1 0 0	25%
	f	1 4 1		3 2		1 2			1 2 1 0	

Table 3.8b. Differences in deviance from logistic regression analysis tests for treatment effects on the proportion of recaptures in the adult females caught (h/f).

	Treatment	
Trap session	Pellets v wheat v GA_3-wheat X^2_2	Feed v control X^2_1
T2	4.084	0.170
T3	0.986	4.091*
T4	1.373	10.701**
T5	0.818	3.867*

* $p<0.05$
** $p<0.01$
For method see Appendix 2d.

Table 3.9a. Numbers of breeding females (r), numbers of adult females (f) and fitted mean percentage values for the proportion of breeding females in the adult females caught, B% = breeding intensity. [$B\%_{(treatment)} = 100\Sigma r_{(treatment)}/\Sigma f_{(treatment)}$].

Trap session		Pellets three banks			$B\%_{(p)}$	Wheat two banks		$B\%_{(w)}$	GA_3-wheat two banks		$B\%_{(ga)}$	$B\%_{(feed)}$	Control four banks				$B\%_{(c)}$
T1	r	1	3	2	13%	3	0	15%	3	8	34%	21%	2	2	0	2	14%
	f	20	13	12		19	1		19	13			19	7	10	6	
T2	r	5	1	0	40%	1	1	40%	0	1	13%	32%	0	0	0	0	0%
	f	10	2	3		1	4		5	3			2	2	0	1	
T3	r	3	8	0	50%	2	3	63%	4	2	55%	54%	0	0	0	0	0%
	f	10	10	2		4			6	5			0	2	1	0	
T4	r	3	2	2	64%	0	0	0%	2	2	67%	58%	0	0	0	0	0%
	f	4	4	3		2	0		3	3			1	0	1	3	
T5	r	0	1	1	33%	1	1	40%	0	2	67%	43%	0	0	0	0	0%
	f	1	4	1		3	2		1	2			1	2	1	0	

Table 3.9b. Differences in deviance from logistic regression analysis tests for treatment effects on the proportion of breeding females in the adult females caught (r/i).

	Treatment	
Trap session	Pellets v wheat v GA_3=wheat X^2_2	Feed v Control X^2_1
T1	5.29	0.80
T2	2.21	3.51
T3	0.38	4.38*
T4	3.82	7.24**
T5	0.93	3.79

* $p < 0.05$
** $p < 0.01$
For method see Appendix 2d.

Table 3.10a. Pooled numbers of breeding females (r), pooled numbers of adult females (f), and fitted values for these pooled data sets for the proportion of breeding females in the adult females caught, B% = breeding intensity. $[B\%_{(treatment)} = 100\Sigma r_{(treatment)}/\Sigma f_{(treatment)}]$.

Trap session		Pellets three banks			$B\%_{(p)}$	Wheat two banks		$B\%_{(w)}$	GA_3-wheat two banks		$B\%_{(ga)}$	$B\%_{(feed)}$	Control four banks				$B\%_{(c)}$
T23	r	8	9	0	26%	3	3	50%	4	3	47%	35%	0	0	0	0	0%
	f	19	12	4		5	7		10	5			2	4	1	1	
T45	r	3	3	3	64%	1	1	33%	2	3	63%	57%	0	0	0	0	0%
	f	4	6	4		4	2		4	4			2	2	2	3	

Table 3.10b. Differences in deviance from logistic regression analysis tests for treatment effects on the pooled data sets for the proportion of breeding females in the adult females caught (r/f).

	Treatment	
	Pellets v wheat v GA_3=wheat	Feed v control
	χ^2_2	χ^2_1
T23	0.04	9.72**
T45	1.77	12.38***

** $p<0.01$
*** $p<0.001$
For method see Appendix 2d.

Table 3:11. Wheat field data for numbers of of breeding females (r), numbers of adult females (f) and fitted mean percentages (BW% = 100Σr/Σf).

Trap session		Wheat field four banks				BW%
TW1	r	0	0	0	0	0%
	f	4	1	3	2	
TW2	r	2	[illegible]	0	1	33%
	f	3	2	2	2	
TW3	r	1	2	0	1	67%
	f	1	2	1	2	

Table 3.12. Variance ratios from tests for differences in slope or intercept in the regression of $\log_e$ weight on $\log_e$ length for males from feeding vs control banks.

Trap session	Slope variance ratio	Intercept variance ratio	Degrees of freedom
T1	1.667	0.349	2, 193
T2	2.412	2.301	2, 157
T3	3.977*	3.440*	2, 74
T4	2.347	1.834	2, 36
T5	2.276	2.387	2, 78

* $p<0.05$

For method see Section 3.2.4.

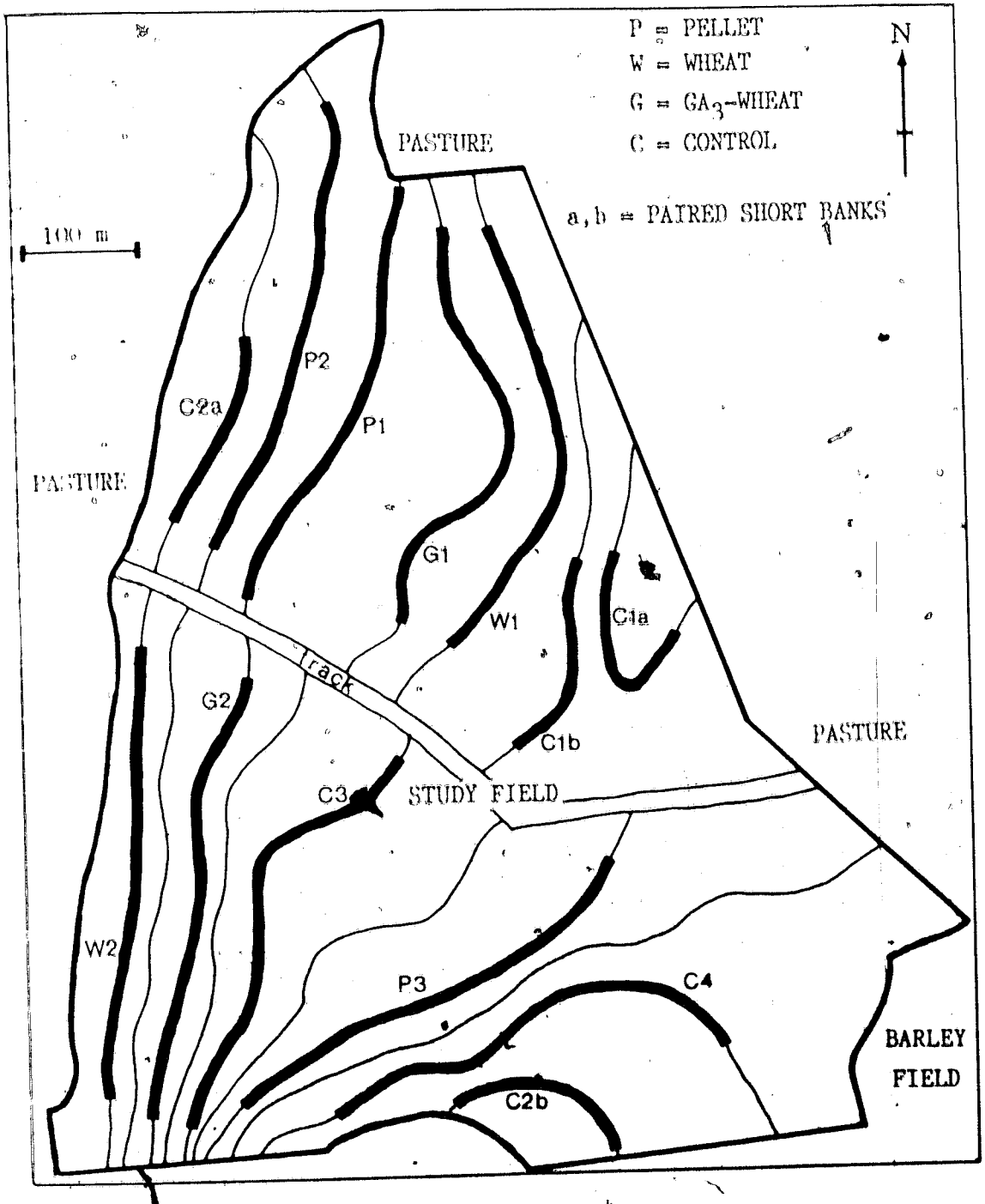


Figure 3.1. Rice field used as the experimental study site.

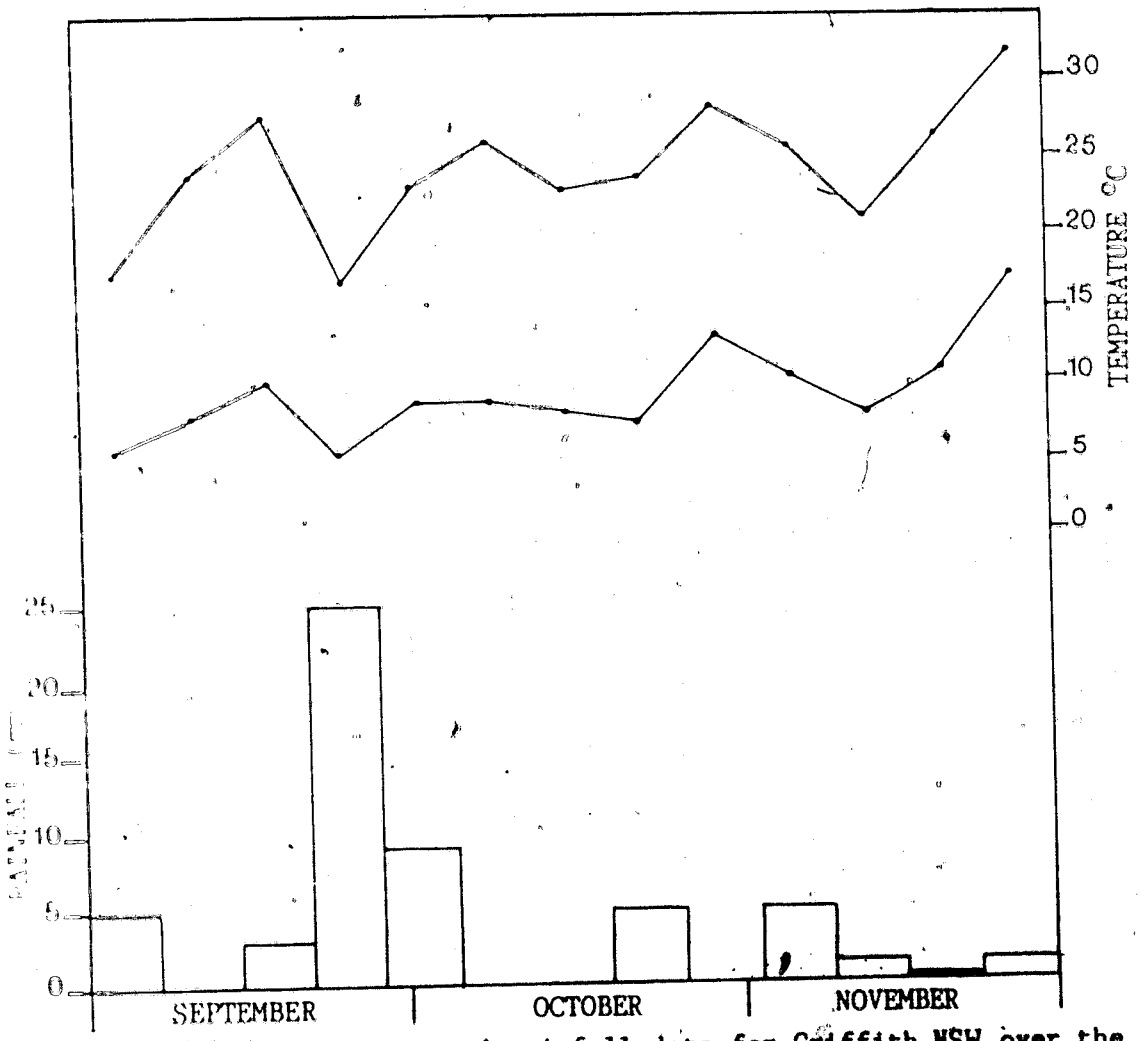


Figure 3.2. Temperature and rainfall data for Griffith NSW over the experimental period September to November 1981. Mean maximum and minimum weekly temperatures are given, and total weekly rainfalls.



Figure 3.3. Mouse visiting a pellet-filled feeder. (Photograph taken by Ed Slater)



Figure 3.4. Many mouse burrows were dug next to feeders and food taken from the feeders could be seen in their entrances.

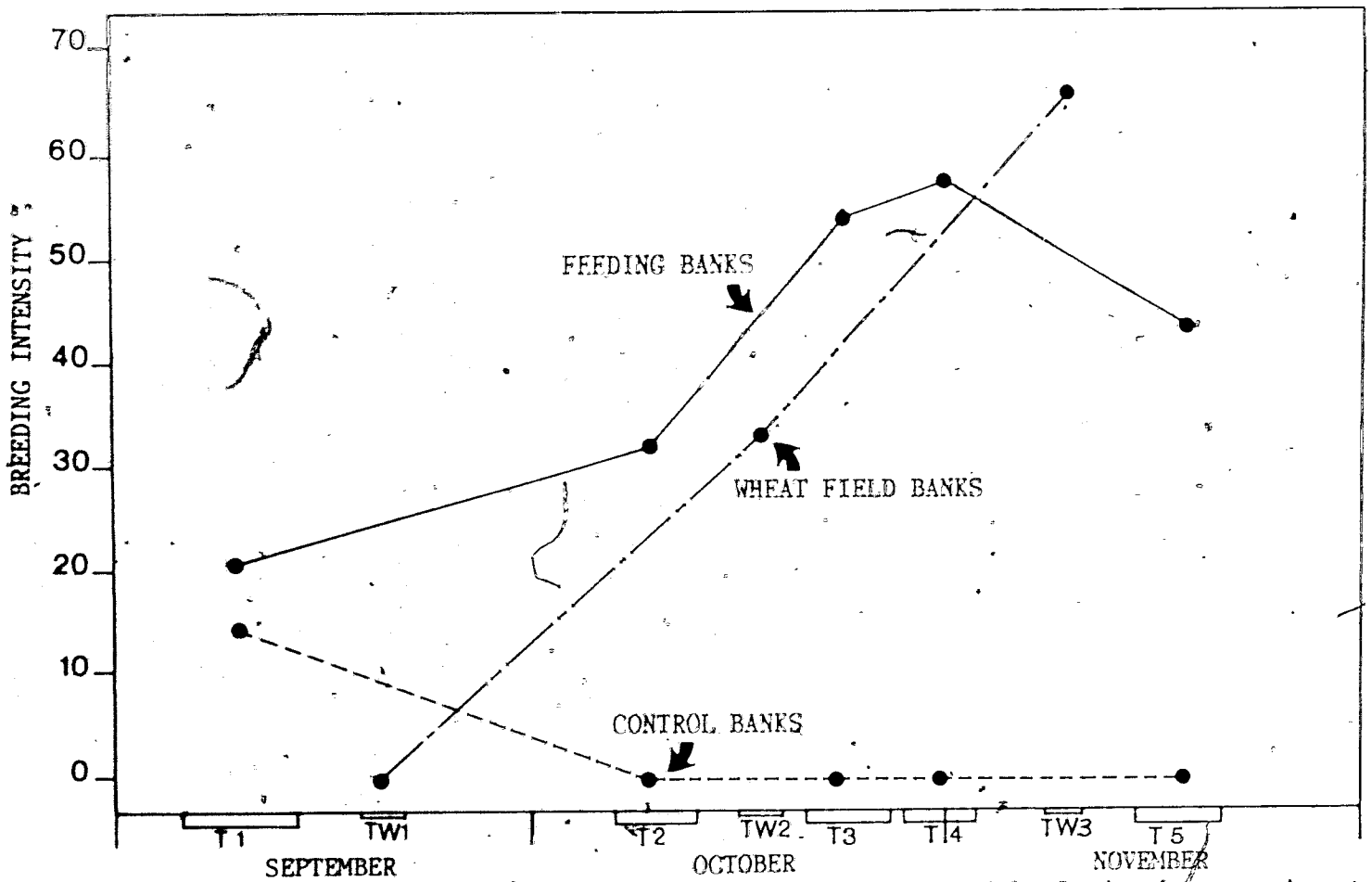


Figure 3.5. Breeding intensity ($100\Sigma r/\Sigma f$) on feeding banks and control banks in the experimental rice field, and also on banks in the neighbouring wheatfield. In the first trap-session there was some breeding on all banks in the rice field. Breeding intensity then increased on feeding banks, but declined to zero on all control banks. In the wheatfield breeding started as normal in October.

CHAPTER FOUR

LABORATORY EXPERIMENTS TO EXAMINE THE ADEQUACY OF RICE-BASED DIETS FOR BREEDING.

4.1. INTRODUCTION

The aim of the experiments described in this chapter was to determine if some of the natural diets eaten by mice on cereal farms (Section 2.3.2.) were adequate in nutritional quality to support reproduction. It was clearly not possible to assess the quality of all the different diets described in Chapter Two, but Bronson's (1979) proposal, that the wide variety of foods usually eaten by mice in the field probably protects them from nutrient deficiencies, indicated that the diets that were the least varied in their composition were the most likely to be nutritionally inadequate. Attention was therefore focussed on these diets. The diet of nearly pure rice eaten by mice in rice stubble fields in autumn seemed the most likely to be inadequate in nutrients needed for reproduction, and it was suggested in Chapter Two that the autumn breeding of mice in rice stubble fields is limited by the poor quality of their food. Therefore most (six out of eight) of the experiments were designed to test whether a diet of pure rice grain is nutritionally inadequate for breeding, and if so, to determine which nutrients are lacking.

Caged mice kept under controlled environmental conditions were used for the experiments described in the present chapter. There were several reasons for choosing to work with caged mice. A problem with high within-treatment variance in breeding intensity was found in the previous field experiment, which reduced the power of this experiment to discern treatment effects. In laboratory experiments conducted under controlled conditions

sources of within-treatment variance can be minimised, and in the experiments described in this chapter, temperature, social factors, sample sizes, and the age, weight and genotype of mice, were controlled within narrow and strictly defined limits to give these experiments strong powers to discern treatment effects. The main disadvantage of laboratory experiments is the limited applicability of their results. Conclusions drawn from experiments conducted on caged mice may not be applicable to mice living in natural environments. Such conclusions therefore need to be tested in the field, but the field experiment need only include feeding treatments which have already been shown to have a significant effect on the breeding performance of caged mice. As the amount of treatment replication possible in the field is limited by the cost and numbers of traps available, the elimination of unsuccessful treatments by preliminary laboratory experiments means that only a small number of different treatments need be tested in the field, allowing a high level of within-treatment replication, and so greatly increasing the power of the field experiment to discern treatment effects.

Ward (1981) in his review of the diet and nutrition of house mice stated 'Little is known about the dietary requirements of the laboratory mouse, and even less about those of wild house mice'. There is plenty of information available on nutrient levels that are adequate to support breeding in populations of caged mice, but there is little information available on their minimum requirements. Previous studies, mainly conducted on laboratory strains of mice, have suggested that breeding performance may be impaired by a lack of protein, minerals or vitamins, or enhanced by the phytohormone GA_3 (Olsen 1981). A brief review of the available information on the house mouse's dietary requirements for reproduction is given below:

1) *Protein.* The minimum dietary requirements of protein for the

reproduction by house mice are not known (Knapka 1984), but thirteen studies were found in which the breeding performance of caged mice was monitored when they were fed diets with different crude protein contents. The results of these studies for two reproductive parameters, mean litter size and mean number of litters produced per female, are summarised in Table 4.1. None of the studies showed statistically significant differences in breeding performance due to diet, but the data in most of them were collected or presented in a way not suited to statistical analysis. As the results of these studies are, however, sometimes quoted as a guide to the protein requirements of mice for reproduction (Ward 1981; Knapka 1983), any changes greater than 10% in either of the above two reproductive parameters are marked on the table, to indicate the effects different dietary protein contents may have on breeding performance. It must be realized though, that these differences in reproductive performance may well be only random effects unrelated to the feeding treatments. Most of the studies were on diets with a high protein content, similar to those in commercial mouse diets or in recommended formula diets for breeding mice (Ford 1977; National Research Council 1978; Ralston Purina Company 1979; Knapka 1983). There no indication that any of the diets imposed a nutritional protein shortage on the mice. Although the diets tested ranged in protein content from 4% to 25%, nearly all the protein concentrations tested allowed a good breeding performance. A poor breeding performance on a low protein diet was reported by only DeMeillon and Paterson (1958), who found only 6% of pairs bred on a 12.8% protein diet, but these results are in contrast to those of Goettsch (1960) who found more than 95% of pairs bred on both 9.4% and 11.4% protein diets. There was some tendency towards poorer breeding on some of the high-protein diets (Howie and Porter 1950; Lee *et al.* 1952; Hoag and Dickie 1960 and 1962). Further evidence for a poor breeding performance of mice fed high protein diets comes from Pleasants *et al.* (1973) who reported a reduced lactation efficiency, indicated

by a lower body weight at weaning, for mice fed a diet with a protein content of 23% compared to controls fed 14% protein.

The amino acid requirements for reproduction have not been reported, but John and Bell (1976) have reported the requirements for the nine amino acids that are essential for growth. They found that mice need only a low concentration of lysine in their diet; less than 40% of the dietary lysine concentration required by laboratory rats. If this low requirement of lysine by mice for growth applies also to their breeding requirements, this could explain why mice can breed so successfully on a grain-based diet, as lysine is the first limiting amino acid in cereal grains.

In summary, the present state of knowledge regarding the protein requirements of house mice for reproduction is sparse, and there is little information available on the minimum requirements necessary for successful breeding.

ii) Fat. Although mice on a fat-free diet become infertile (Decker *et al.* 1950), the dietary requirements for fat are probably low. Hoag and Dickie (1960 and 1962) found 6% fat, the lowest concentration they tried, was adequate for reproduction and Knapka *et al.* (1977) found that a diet with a fat content as low as 4% did not impair reproductive performance or weanling growth. Minimum requirements may be even lower, as Bosshardt *et al.* (1950) found that mice require no more than 0.5% dietary fat for growth if they are given adequate vitamin B_{12}. One or other of the fatty acids linoleic or arachidonic acid are essential for mice (Knapka 1983), but they apparently have some ability to store these in their bodies (Cerecedo *et al.* 1952).

iii) Vitamins. Mice require a dietary source of the B-complex vitamins and vitamins A, D and E. The minimum requirements for successful reproduction are not known but lists have been pub-

lished of amounts that have proved satisfactory for breeding mice in laboratories (Ford 1977; National Research Council 1978; Knapka 1983). Mice do not require a dietary source of vitamin K (Knapka 1983) or vitamin C (Ball and Barnes 1941) as they are synthesized in adequate quantities by their intestinal micro-organisms. A deficiency in vitamin A will cause sterility, associated in females with persistent cornification of the uterus (Wolfe and Salter 1931; McCarthy and Cerecedo 1952; Dam and Søndergaard 1964; Green 1970).

iv) Minerals. The minimum mineral requirements for successful reproduction are not known, but levels that have produced acceptable breeding performance in caged mice have been published (National Research Council 1978; Knapka 1983).

v) Chemical stimulants and inhibitors. These factors have been discussed previously in Section 2.4. Diets containing milk-ripe seeds, or other actively growing green plant tissue, may contain chemicals that actively promote breeding, such as GA_3 and 6-MBOA. Mature seeds do not usually contain these substances. Further, particular plants may contain chemicals which act as antifertility agents.

In summary, there is little known about minimum requirements for almost any nutrients needed by house mice for breeding, and the little that is known is of doubtful applicability to the wild strain mice being investigated in the present study. Mice of different strains vary markedly in their response to different nutritional deficiencies (Fenton and Cowgill 1947a,b; Cerecedo *et al.* 1952; McCarthy and Cerecedo 1952; Hoag and Dickie 1960), and Knapka (1983) suggests that this may be one cause of the lack of consistency in the results of different studies on mouse nutrient requirements. He suggests the other main cause is the different experimental conditions used in different studies. It is clear

also, that the requirements for any particular nutrient may be affected by the availability of other nutrients. For example, Nelson and Evans (1953) found that the protein requirements of laboratory rats for breeding are closely linked to the concentration of the B-complex vitamins in their diet. They found that rats on low protein diets (5%) bred far more successfully when they were given double the standard B-vitamin allowance, whereas rats on 10% protein diets bred just as well on the standard B-complex vitamin allowance. Such relationships are probably also true for mice.

The scarcity and ambiguity of this available information on minimum nutrient requirements for house mouse reproduction, meant it was not possible to assess, *a priori*, the nutritional adequacy of the natural diets described in Section 2.3.2., or to determine which nutrients are limiting for reproduction in these diets. But, to get an indication which nutrients are likely to be lacking in a diet of pure rice, the nutrient composition of diets used successfully to support breeding in the studies reviewed above, is compared below to the nutrient composition of rice grain reported by Grist (1975).

The protein contents tested in most of the studies in Table 4.1 would be much higher than that of rice, which has an average protein content of only about 8%. Therefore protein is clearly one of the nutrients likely to be undersupplied. A comparison of the minerals in rice grain with mouse requirements for growth and reproduction (National Research Council 1978), is presented in Table 4.2. These data suggest calcium, zinc, chromium, manganese and copper may be lacking in rice grain, but these are rough estimates only. Rice is rich in B-complex vitamins and vitamin E, so these are likely to be adequately supplied. Rice contains only negligible quantities of vitmins A and D, and mice eating a pure rice diet could be expected to be deficient in vitamin A.

Whether mice eating a rice diet in the field would have adequate vitamin D is unclear. Ergsterol, the progenitor of vitamin D_2 is the main sterol in many fungi (Green 1970), and spilt rice grains in stubble fields were often mouldy. Exposure of these moulds to sunlight might have resulted in the conversion of ergsterol to Vitamin D_2. The extent to which mice leave their burrows during daylight, and expose themselves to sunlight, so they can manufacture their own vitamin D, and eliminate a dietary requirement for this vitamin is also uncertain. Mature rice grain would contain no GA_3 (Osada *et al.* 1973; Kurogoshi *et al.* 1979), so this phytohormone may be limiting if a dietary source improves breeding.

As there are about fifty nutrients essential for house mouse reproduction (Knapka 1983), and as nutrients may interact so that the quantity of one nutrient in the diet may affect the requirements for others (Russel 1948; Bosshardt *et al.* 1946 and 1948; Knapka *et al.* 1977; National Research Council 1978), the problem of finding a limiting nutrient was potentially complex. Only a few tests could be conducted, so it was decided that the aim of this section could best be met by initially testing some of the natural supplements that mice include in their grain diets, to see if these foods improve breeding performance. Natural supplements provide a broad spectrum of nutrients, and so were considered more likely to improve breeding performance, than supplements of isolated nutrients. The results of these tests could then be used as a basis for selecting individual nutrients or chemicals to use in further tests on limiting dietary factors for breeding. The supplements chosen were 1) foods eaten by mice in the field, or similar substitutes, 2) rich in one or more nutrients that were thought likely to be limiting for breeding, 3) palatable to mice, 4) available in the laboratory. Mealworms were chosen because they are rich in protein, and contain some vitamin A, and because mice consistently include a small invertebrate supplement in their predominantly grain diets. Milk-ripe

grain was chosen because it is rich in GA_3 and vitamin A, and because breeding started just after mice had switched to a diet containing large quantities of this food. Rice sprouts were chosen because experiments with voles (*Microtus montanus*) had shown their breeding was stimulated by the addition of a sprout supplement to their diet which suggested they contained a stimulatory chemical (Pinter and Negus 1965). Sprouting of cereal grains causes an increase in their content of GA_3 (Murakami 1960; Groat and Briggs 1969; Osada *et al.* 1973; Jones and Stoddart 1977), 6-MBOA (Pinter and Negus 1965; Sanders *et al.* 1981), and many nutrients, including protein (Lemar and Swanson 1976; Millar 1977; Hamad and Fields 1979; Lorenz 1980), Vitamin A (Miller 1977; Lorenz 1980) and B-complex vitamins (Cheldelin and Lane 1943; Lemar and Swanson 1976). The pure nutrients that were tested in addition to the natural food supplements were protein, vitamin A and GA_3. These supplements were added to a rice grain diet.

The decision was taken to use only wild-strain mice, despite their genotypic variation, because it is well documented that mice of different genetic strains have different nutrient requirements for growth and reproduction (Fenton and Cowgill 1947b; Fenton and Carr 1951; Cerecedo *et al.* 1952; Hoag and Dickie 1960; Goodrick 1973; Truscott *et al.* 1974; Wodzicka-Tomaszewska *et al.* 1974; National Research Council 1978; Roberts 1981). Hence conclusions drawn from the results on experiments conducted on wild mice, could be more validly applied to natural populations than conclusions drawn from work on laboratory strains.

4.2. METHODS

4.2.1. Animal house and cages

All mice were kept in a single climate-controlled room at the CSIRO Division of Wildlife and Rangelands Research animal house in Canberra. For the duration of the study photoperiod was set at 14 h light, 10 h dark, and temperature at 23±1°C.

All cages were made of black polypropylene with clip-on wire tops. The cages measured 18 x 23 cm in the base and were 14 cm high. Water was provided *ad libitum* in glass dropper-bottles. Tissue paper was provided for bedding. All mice not on experimental treatments were given commercial mouse pellets *ad libitum*. (These were the same pellets as those used in the field experiment, and their analysis is given in Appendix 1. They are hereafter called 'pellets'). Cages were stacked on racks, with four shelves per rack. During experiments cages with mice receiving different treatments were all randomly mixed on the shelves. This was to ensure that any pheromonal or other signals which might affect the breeding performance of neighbouring mice were randomized across all treatments.

4.2.2. Experimental mice

All mice used in feeding experiments were either trapped in rice stubble on farms in the MIR, or were the first generation offspring of such mice. The latter group were produced from wild-caught mice that were kept in breeding pairs and fed a pellet diet. The litters from these breeding pairs were kept in the parental cage until they were three weeks of age, and then were ear-tagged and removed from the parental cage. All males were allocated individual cages, females were kept in groups of

three. Mice were only used for a single experiment, after which they were killed. In Experiments 4, 6 and 7, wild-caught mice of unknown age were used. In the other experiments mice born in the animal house were used.

Wild-caught mice would not breed when they were first brought into the animal house, so they were given a period of four to ten weeks to adjust to cage life, before being either subjected to experimental feeding, or being paired for breeding. Even after this adjustment period, only about 70% of pairs of wild-caught mice fed pellet diets bred successfully. In the pairs of mice that were infertile, the males always had decended testes and motile sperm, but the females often had closed vaginae, and autopsies usually revealed threadlike uteri. Wallace (1981) suggested that a lack of exercise promotes infertility in caged mice and that it can be cured by provision of exercise wheels. The cages available for the present study were unsuitable for the attachment of wheels, but many mice were observed to exercise by looping-the-loop between the cage floor, wall and roof, and would perform more than forty such loops in a minute. This presumably provided the same type of exercise as a wheel, so it seems unlikely that lack of exercise caused the infertility. Mice born in the animal house were more fertile than wild-caught mice, with about 90% of mated pairs breeding when they were fed pellet diets.

During experiments, the pre-littering mortality of mice was zero except for the mice fed wheat plants in Experiment 1. But adult males sometimes died soon after litters were born, presumably killed by the females which are known to become particularly aggressive around the time of parturition (Brown 1953). Only in Experiment 6 were there deaths of adult females, and this is thought to be a result of a nutritional deficiency in their experimental diet (Section 4.3).

4.2.3. Assignment of mice to diet treatment groups

Method A. (Used for Experiments 4, 6 and 7.) Wild-caught mice of unknown age were used. In all experiments the minimum weight of mice at the start of the feeding treatments was 10.0 g for females, and 14.0 g for males. The minimum head-body length was 74 mm for females and 84 mm for males.

In Experiment 4, mice were allowed to adjust to laboratory conditions for a period of five weeks. Then any mice with wounds or bald patches were rejected. The remaining individuals were ear-tagged, weighed and measured for head-body length. Individuals were then listed in order of decending body weights, with a separate list being prepared for each sex. The five heaviest mice on each list were then randomly assigned to each of the five experimental treatments. Then the next five individuals on each list were assigned to the five treatments, and so on down the lists, until twelve mice of each sex had been allocated to each treatment group. This gave a male and a female list for each treatment, with twelve mice listed in order of decending body weight on each list. Mates were then assigned within treatment groups by pairing males and females from the top of each list down, so that members of each mated pair had similar body weights. An alternative method of pairing the mice would have been to randomly match the males and females assigned to each treatment. This was not done because previous experience had shown that large males often killed or wounded small females when they were caged together, but rarely injured females close to their own weight. The mice used in Experiments 6 and 7 were all from the same wild stock. They were allowed to adjust to laboratory conditions for ten weeks after capture and then sorted into eight treatment groups by the same method as Experiment 4. Four of these groups, each of 22 pairs, were used as treatment groups for Experiment 6, and three groups, each of 23 pairs, were used for Experiment 7. The remaining group was used for the control treatment for both experiments (pure rice diet), but one pair was excluded from the analysis of the Experiment 6 results to match sample sizes.

This method of assigning mice to diet groups, ensured that the mean weight of mice was closely matched across the different groups. As the weight of these mice was closely correlated with head-body length this parameter was also closely matched across groups.

Method B (Used for Experiments 1 and 2). Mice which had been born in the animal house were used. As there were only two treatments in each of these experments it was possible to divide litters equally, and so match the age distributions and parentage of the two treatment groups in each experiment. Mice from each litter were sorted into single-sex pairs, and then the members of the pair were randomly assigned to each of the two treatment groups. Four lists were drawn up; a male and a female list for each diet group. Mice on these lists were then arranged in order of decending body weight, and mates were assigned by pairing males and females from the top of each list down. Sibling matings were avoided by slightly shifting the position of mice on the lists if siblings were otherwise matched together.

Method C (Used for Experiment 3). This was the same as Method B, but only females were used, and they were caged individually.

Method D. (Used for Experiment 5 and 8). Mice born in the animal house were used, but as there were four treatment groups it was not possible to split litters evenly, as few litters had four mice of the same sex. Therefore Method A was followed, but sibling matings were avoided, as in Method B.

The ages and body weights of laboratory-born mice at the start of feeding treatments in the above experiments are presented in Table 4.2. After mice had been assigned to treatments and mating pairs, by one of the above methods, females were caged in

groups of three which had been assigned to the same treatment, and males were caged individually. Experimental feeding then started. After four weeks, the females were removed from their group cages and placed with their assigned mates. Experimental feeding was then continued for the duration of the experiment.

4.2.4. Data collection and analysis

The experiments were designed to measure the effects of different diets on breeding performance. Breeding intensity, which was proportion of females that produced a litter, and mean first litter size were the measures of breeding performance in these tests. Cages were checked for litters at least every second day. Only first litters were included in the litter size measurements, as there was insufficient time available to get adequate sample sizes of second or third litters. The only exception was Experiment 4, for which the data for the proportion of females producing second and third litters were also analysed. Body weights and lengths of mice were measured at intervals through the duration of the experiments.

Data for breeding intensity were analysed for treatment effects by logistic regression (Section 3.2.4). Data for litter sizes could not be analysed by standard analysis of variance, because of the unequal sample sizes, so tests for treatment effects were conducted by analysis of deviance, by fitting generalized linear models to the data, using the identity link function, and an assumed normal distribution of errors (McCullagh and Nelder 1983). An example is presented in Appendix 2e.

4.3. Description of diets, results and conclusions

All rice used in the experiments was husked long grain rice of the inga variety, supplied by Rice Growers Co-operative Mills Ltd. of Griffith, NSW. This rice was fungicide and pesticide free. All pellets used were the commercial pellets described in Appendix 1. When pellets or rice were included in a diet they were always fed *ad libitum* ration. All food supplements were provided fresh each day, and were fed to the mice about an hour before the 10 h dark period started. Drinking water was changed every three days, and any supplements added to the drinking water were freshly mixed at these times. The protein content of foods (on a dry basis) was determined by the method described in Section 2.2.8. The protein content of the inga rice was 8.8% and of the pellets was 25.1%.

Experiment 1.

Diets

Diet 1.1 = wheat plants
Diet 1.2 = milk-ripe barley grass seeds

These diets were chosen to compare the two main foods eaten by mice in spring wheat fields. Wheat plants are the main food in August, before grass seeds ripen, and milk-ripe barley grass seeds are the main food in September, when the mice come into breeding condition.

Both the wheat plants and the barley grass seeds were collected on a rice farm in September. The wheat plants were at a stage just before the panicle emerged and were cut off about 3 cm

above ground level. The barley grass was at the milk-ripe stage and whole panicles were collected. Both these foods were deep frozen within two hours of collection and were still frozen when given to the mice. The mice were given both foods *ad libitum*. The barley grass seed had a protein content of 21.0% and the wheat plants 2.6%.

Results

Data for body weights are presented in Table 4.4. Within three days of the start of the wheat plant feeding treatment, mice had lost an average of 20% of their body weight. On the fourth day, three females and one male were dead, and all carcasses had been chewed by the cage mate. The surviving mice were slow in their movements, and some had low body temperatures. These survivors were switched to a pellet diet, and they made a rapid recovery. Mice fed the barley grass diet lost an average of 8% body weight over the first three days on the diet, but by the twentieth day this had been regained. All females had imperforate vaginae at the start of the experiment, and none became perforate during the experiment. There were no visible pregnancies at autopsy on day 20.

Conclusions

The wheat plant diet was inadequate to meet maintenance energy requirements. Possibly the mice fed this diet had unsuitable intestinal microflora to properly digest it, and if they had been given a period of adjustment they might have faired better. The supplements of seeds and insects mice in the field include in their diet when they eat wheat plants are probably sufficiently high in energy content to allow them to maintain

body weight. The barley grass diet was apparently adequate to meet maintenance energy requirements once mice had adjusted to it, but there was no indication of whether it supplied enough nutrients or energy to meet breeding requirements.

Experiment 2.

Diets

Diet 2.1 = pellets
Diet 2.2 = pellets + milk-ripe wheat seeds

This experiment was designed to test whether the inclusion of milk-ripe seeds in an otherwise balanced diet stimulates breeding.

The milk-ripe wheat was collected as whole panicles on a rice farm in October, and was deep-frozen within two hours of collection. Each mouse was given one frozen panicle a day. The mean dry weight of endosperm in a panicle was about one gram, and mice ate almost all this endosperm.

Results

Data for body weights and testes weights are presented in Table 4.5. There were clearly no treatment effects on either male body weights or testes weights. Female body weights at the end of the experiment are not given, as the inclusion of pregnant and lactating females in the samples would have confused the interpretation of these data.

The data for reproductive performance are also presented in

Table 4.5. . Breeding intensity was slightly higher on the unsupplemented pellet diet, though not significantly so ($\chi^2_1 = 1.890$, $p>0.1$). There was clearly no difference between diets in mean litter size. It is therefore concluded that the supplement of milk-ripe wheat did not improve breeding performance.

Conclusions

On rice farms, mice started breeding about a month after milk-ripe seeds were included in their diet (Figure 2.12), and it was suggested that this effect was possibly due to some chemical factor such as GA_3 present in these seeds which stimulated breeding (Section 2.4). The failure of a milk-ripe seed supplement to improve breeding performance in the present experiment is evidence against the presence of such a chemical stimulant for breeding in this food. While it is possible such a stimulant was present, but supplied in a dose too small to stimulate the mice in this experiment, this is unlikely because both Olsen (1981) and Sanders *et al.* (1981) found only very small amounts of such stimulants are adequate.

Experiment 3

Diets

Diet 3.1 = mature rice grain
Diet 3.2 = milk-ripe rice grain

This experiment was designed to test whether a diet consisting only of milk-ripe seeds stimulated a response in the reproductive organs of female mice. Panicles of milk-ripe inga rice were collected on a rice farm in early March, and frozen until use. The panicles were about half their ripe weight at this

stage. Panicles of mature rice were collected from the same crop a month later. Average protein contents were 8.8% for mature rice grain and 9.0% for milk-ripe rice grain. Both foods were provided *ad libitum*.

Results

Data for mean body weight, ovarian weight and uterine weight are presented in Table 4.6. There were clearly no treatment effects on any of these data.

Conclusions

In Experiment 2 it was suggested that milk-ripe seeds given as a supplement might contain an insufficient dose of any chemical that might stimulate breeding to be effective. To obviate this problem milk-ripe seeds were given as the sole food in the present experiment. It was unlikely that any nutrient deficiency sufficient to inhibit breeding would develop during the short term duration of the experiment. The failure of this diet to increase ovarian or uterine weights is additional evidence that milk-ripe grain does not contain a substance that stimulates breeding in house mice.

Experiment 4

Diets

Diet 4.1 = rice grain
Diet 4.2 = rice grain + rice sprouts
Diet 4.3 = rice grain + mealworms
Diet 4.4 = rice grain + rice sprouts + mealworms
Diet 4.5 = pellets

The aim was to test whether these supplements improved the nutritional quality of a rice grain diet sufficiently to improve breeding performance, and to see if these supplemented diets were as adequate as a balanced pellet diet. The protein content of the rice grain was 8.8% and of the sprouted rice grain was 9.5%.

Mealworms were kept in rice bran with carrots and brewer's yeast. Only final instar, live mealworms were fed to mice. The average fresh weight of a mealworm was 0.16 g, the dry weight 0.04g, and the protein content was 50.6%. Initially the mealworms were fed at a rate of two per mouse per day, but as most of these were left uneaten, this ration was cut back to one mealworm per day. In some cages this entire ration was eaten, but in others only about a third of the mealworms were eaten.

Rice sprouts were grown in 9 cm petri dishes from unhusked inga rice. The rice grain was first soaked in a 2% solution of sodium hypochlorite for 30 minutes to destroy any fungal spores, and then rinsed ten times in distilled water. The petri dish bases were spread with a triple layer of filter paper and this was saturated with distilled water. Ten grams (dry basis) of rice grain was then spread on the filter paper, and then covered with the petri dish lid, placed in an oven at 27°C and kept saturated with distilled water for 6 to 10 days. After this time they were 2 to 4 cm high. Fresh sprouts were rinsed and fed to the mice. Each pair received about 4 g (fresh blotted weight) of sprouts (about 80 sprouted grains) daily. The mice nearly always ate all the endosperm left in the grain, but they ate relatively little of the shoot or root material.

Results

Data for body weights and reproductive performance are pre-

sented in Table 4.7. The analysis of variance of the body weights of males at the end of the experiment, after 109 days on the experimental diets, revealed a significant treatment effect due to supplementation with mealworms ($F_{1,45} = 4.12$, $p<0.05$), but not due to rice sprouts ($F_{1,46} = 0.00$, $p>0.1$), and there was no interaction between these two supplements ($F_{1,44} = 0.39$, $p>0.1$). By day 109 no females fed the pure rice diet had produced litters, but on the other four diets about half the females had litters. No females produced more than one litter. Breeding intensity was significantly improved by supplements of rice sprouts ($\chi^2_1 = 4.564$, $p<0.05$), but not by supplements of mealworms ($\chi^2_1 = 2.545$, $p>0.05$). There was clearly no difference in breeding intensity between the pellet diet and the supplemented diets. Litter sizes clearly did not differ between the three supplemented rice diets. They were slightly larger on the pellet diet, but not significantly so ($F_{1,21} = 2.92$, $p>0.05$).

Conclusions

These results suggest that a pure rice diet is inadequate to support breeding, but that supplementation with rice sprouts makes it as adequate as a balanced commercial diet.

Experiment 5

Diets

Diet 5.1 = pellets
Diet 5.2 = pellets + rice sprouts
Diet 5.3 = rice grain
Diet 5.4 = rice grain + rice sprouts

This experiment tested whether a supplement of rice sprouts improves the breeding performance of mice eating mature rice grain or pellets. The rice and rice sprout allowance was the same as for Experiment 4.

Results

Data for body weights and reproductive performance are presented in Table 4.8. Standard errors around the means are sufficiently large to indicate that there were no significant differences in body weight between the different feeding groups for either sex by day forty of the feeding treatment. The breeding intensity of mice on the pellet based diets was not improved by the rice sprout supplement, but breeding intensity of mice on rice based diets was significantly improved, both for the proportion of females producing first litters ($\chi^2_1 = 4.557$, $p<0.05$) and for the proportion producing second litters ($\chi^2_1 = 4.857$, $p<0.05$). Standard errors around mean litter sizes are sufficiently large to indicate that there was no significant increase in litter size due to the sprout supplement for either rice or pellet fed mice. The breeding intensity of mice fed the sprout-supplemented rice diet was not significantly different to that of mice fed pellets for the production of first litters ($\chi^2_1 = 1.471$, $p>0.1$), or second litters ($\chi^2_1 = 2.348$, $p>0.1$), but there was a significantly lower breeding intensity in the proportion producing third litters ($\chi^2_1 = 4.557$, $p<0.05$).

Conclusions

Supplements of rice sprouts caused a significant increase in breeding intensity in both Experiment 4 and the present experiment. The improvements in the nutritional quality in grains associated with germination include increases in the content of

GA_3, 6-MBOA, protein, and several vitamins (Section 4.1). The uniformly high breeding performance of mice on the pellet diets, with or without the sprout supplement, indicates that the substance present in sprouts was not limiting for breeding for mice on pellet diets. A chemical stimulus could be expected to improve the breeding performance of mice on both the rice and pellet diets. For example, Olsen's (1981) mice in her GA_3 experiments were fed pellet diets. A nutrient additive, in contrast, would probably only improve the breeding of mice on the rice diet, as mice on the pellet diet should already have had all their nutrient requirements met. The amount of sprouts included in the diet was only small, so only slight changes in the protein content of the rice diet would have occurred, probably less than a 1% increase, so it seems unlikely that a change in protein was responsible. As the sprouts were grown in distilled water, it is unlikely there mineral content would have changed appreciably. This leaves vitamins as likely candidates responsible for the improved breeding performance. Vitamin deficiencies can either be directly limiting, or they can affect the requirements for other nutrients (Section 4.1). That significantly fewer of the females on the sprout-supplemented rice diet produced third litters than those on the pellet diet, suggests that the sprout supplemented diet was inferior to the pellet diet.

Experiment 6

Diets

Diet 6.1 = rice grain
Diet 6.2 = rice grain + casein
Diet 6.3 = rice grain + vitamin A
Diet 6.4 = rice grain + casein + vitamin A
Diet 6.5 = rice grain + casein + vitamin A + GA_3

This experiment tested whether rice grain was limiting either in protein or vitamin A for breeding, and also tested the effects of GA_3 on breeding performance.

Casein was provided as a source of high-quality protein, as its amino acid profile is complementary to that of rice protein (Food and Agriculture Organization 1970). The casein was in a soluble powder form as spray-dried sodium caseinate, supplied by Amalgamated Co-operative Marketers (Australia) Ltd. It contained a minimum of 92% protein, and a maximum of 1.5% fat on a dry basis. Using the following method, the casein was combined with the rice to form a crumble. Twenty-two kilograms of rice were ground up to a coarse flour and this was thoroughly mixed with 3 kg of casein. A small quantity of cold, distilled water was sprinkled over the mixture, and worked in by hand, until crumbs about 1 cm in diameter were formed. This crumble was spread thinly on trays and dried at 25°C. The crumble was expected to contain a minimum of 18.0% protein (dry basis), and a Kjeldahl assay gave the protein content as 18.5%.

Vitamin A was added to the drinking water. The contents of one capsule, containing 10000 i.u. of water-soluble vitamin A from beta-carotene, was added to each litre of water. These capsules were produced by Nature's Way Health Products of Victoria. GA_3 was also added to the drinking water. The GA_3 was produced by Calbiochem-Behring Corp., La Jolla, California, as a potassium salt of GA_3 ($C_{19}H_{21}KO_6$) mixed with 20% inert ingredients. A standard solution of 10^{-4}M GA_3 solution was made up by dissolving 42.2 mg of this salt preparation in one litre of water. For mice receiving GA_3 and vitamin A, one millilitre of this standard added to 999 ml of the vitamin A solution described above, gave one litre of drinking water with 10,000 i.u, Vitamin A and a GA_3 concentration of 10^{-7}M.

Results

Data for body weights and reproductive performance are presented in Table 4.9a. After 30 days on the experimental diets there were no significant treatments effects on the mean body weights of mice of either sex.

Breeding data for diets 6.1, 6.2, 6.3 and 6.4 were analysed for treatment effects on breeding performance due to casein, vitamin A, or the interaction of these two factors. The results are presented in Table 4.9b. Breeding data for diets 6.4 and 6.5 were analysed for treatment effects due to GA_3 and these results are also presented in Table 4.9b. Casein supplementation had a highly significant effect on both breeding intensity (χ^2_1 = 7.072, $p<0.01$) and mean litter size ($F_{1,44}$ = 18.29, $p< 0.001$). Neither Vitamin A nor GA_3 affected breeding intensity or litter size.

The data on breeding performance for diets 6.2, 6.4 and 6.5, the diets supplemented with casein, were then pooled. As neither vitamin A nor GA_3 significantly affected breeding performance, these treatments were ignored in the following analysis. A logistic regression analysis was conducted to test whether the females' initial body weight or initial condition index ($\log_e$ weight/$\log_e$ length) at the start of the experiment, differed between females that later produced litters and those that did not. Neither initial weight (χ^2_1 = 0.579, $p> 0.1$), nor initial condition index (χ^2_1 = 1.309, $p> 0.1$) significantly affected whether or not females produced a litter.

Conclusions

Protein, vitamin A and GA_3 were chosen because they were

absent or in very low quantities in rice, and were thought likely to have an effect on breeding. The results clearly indicate that protein was the limiting nutrient in the rice diet. The inadequacies of cereal protein to meet the requirements of reproduction have been discussed in Section 2.4, as have the effects of protein restriction on inhibiting endocrine secretion and ovarian function (Section 1.1), but the minimum requirements of protein for house mouse reproduction are unknown (Section 4.1). Protein is required in large quantities for the growth of placental and foetal tissue, and for the production of milk, so maternal stores of protein could only meet breeding requirements to a limited extent.

That nutrients other than protein were also inadequate in these diets, was suggested by the deaths of lactating females and by the failure of some mice to breed even on the casein supplemented diet. Thirty-two percent of the females fed diets with the casein supplement died in the late stages of lactation, compared to only 2% of females in this experiment on non-casein diets, and 3% in Experiment 6 which had mice caught at the same time but fed non-casein diets. The cause of these deaths was unknown. Before death the mice moved slowly, had low body temperatures, and some showed vaginal or rectal haemorrhaging. *Post mortem* examinations (kindly conducted by Dr Simon Bain, veterinary surgeon of the John Curtin School of Medical Research, Australian National University) showed apparently normal viscera. Neither the males, nor the offspring showed any adverse reaction to the casein, and the proportion of young that survived to weaning on casein supplemented diets was no lower than those on the other diets, even though some mothers died when the young were only 14 days old. It seems likely that the supplementary protein led to a deficiency of some other nutrient, and that the females were unable to cope with this deficiency during late lactation when nutritional demands peak. A possible cause is

suggested by the finding of Dubos *et al.* (1968), that a casein-starch diet which contains only 0.05% magnesium is adequate for growth of mice, but causes sudden death in some females during lactation

The lack of a breeding response to the vitamin A supplement, indicates that the mice had adequate body stores of this substance to meet breeding requirements over the short term duration of this experiment (109 days), as rice grain contains negligible quantities of vitamin A (Section 4.4). It is well documented that an extended period on a vitamin A-free diet causes infertility (Section 4.1). In the mice used in the present experiment there was no sign of any of the vitamin A deficiency symptoms described by Wolfe and Salter (1931) or McCarthy and Cerecedo (1952). The failure of GA_3 to stimulate breeding was in contrast to Olsen's (1981) findings, but in her experiment the control mice had a low breeding intensity, whereas in the present experiment the control mice (Diet 64) had a high breeding intensity, leaving little room for improvement.

One of the ways in which nutrition can affect breeding performance is by altering body weight, or other measures of body condition. Redhead used $\log_e$ weight adjusted for $\log_e$ length as a measure of condition index (Section 3.2.4), and suggested this index affected the breeding performance of mice on MIR farms. There was no evidence that this index affected breeding in the present experiment.

Experiment 7

Diets

Diet 7.1 = rice grain
Diet 7.2 = rice grain + mealworms
Diet 7.3 = rice grain + milk-ripe rice grain
Diet 7.4 = rice grain + mealworms + milk-ripe rice grain

This experiment was conducted to re-test the effects of natural supplements to rice diets, to confirm conclusions drawn from the previous experiments. Mealworms were provided for the mice as for Experiment 4, but the ration was one mealworm per mouse per day from the start of exerimental feeding. Milk-ripe inga rice was used, as in Experiment 3, but the ration was two frozen panicles for each mouse a night. This provided each mouse with an average of 2.0 g fresh weight of milk-ripe endosperm per day. Mice almost always ate all the endosperm provided.

Results

Data for body weights and breeding performance are presented in Table 4.10a. Standard errors around the mean body weights on day thirty of the feeding treatment are sufficiently large to indicate there were no treatment effects on body weight for either sex. The results of the analysis of the breeding data are presented in Table 4.10b. ~~Only one~~ female each on diets 7.2 and 7.4 had second litters, so only data for first litters was analysed. There were no treatment effects on either breeding intensity or litter size.

Conclusions

Mealworms did not affect breeding performance, a finding in agreement with the results of Experiment 4. The inclusion of milk-ripe grain in the diet did not affect either testes weights (Experiment 2), ovarian or uterine weights (Experiment 3), or breeding intensity or litter size (Experiment 2 and the present experiment). These uniform results are strong evidence against the presence of a chemical stimulus for breeding in milk-ripe grain, a posibility suggested by the findings in Chapter Two, and earlier by Olsen (1981). While milk-ripe seeds are richer in some vitamins than mature seeds, there is no evidence from these experiments that this difference is sufficient to affect breeding performance.

Experiment 8

Diets

Diet 8.1 = rice grain
Diet 8.2 = oat grain
Diet 8.3 = oat grain + sunflower seeds
Diet 8.4 = pellets

For the future field experiment, a seed food that was palatable to mice, and of sufficient nutrient quality to support a good breeding performance was required. This final experiment tested the breeding performance of mice fed rice and other seeds, to determine the suitability of these seeds as supplements to improve the diet quality of mice eating a rice diet in a future field experiment. The aim was to find a seed diet that would give a breeding performance as good as a pellet diet. Although pellets and rice/casein crumble are both nutritious foods which

support a good breeding performance, they are not palatable to mice, and given a choice between these foods and rice grain, mice would almost invariably eat the latter food despite its inferior nutrient quality (pers. obs.). Sage (1981) also found mice preferred grain (canary seed) to pellets.

The oat grains and the sunflower seeds were unhusked, but the mice removed the husks. Husked oats had a protein content of 11.6%, and husked sunflower seeds of 22.2%. All diets were fed *ad libitum*.

Results

Data for body weights and reproductive performance are presented in Table 4.11. There were no treatment effects on body weights of females by day 60, but male body weights significantly heavier for the pellet fed mice ($F_{1,52} = 8.08$, $p<0.01$).

No females had perforate vaginae at the start of the feeding treatment, and all were probably pre-pubertal. By day 70 there was a lower proportion of females with perforate vaginae on the rice diet than on the other diets ($\chi^2_1 = 7.229$, $p<0.01$). Breeding intensity was lower on the rice diet than on either the oats diet ($\chi^2_1 = 7.228$, $p<0.01$) or the oats and sunflower diet ($\chi^2_1 = 15.97$, $p<0.001$). But the breeding intensity of mice on the pellet diet was not significantly different from that of mice on the oats and sunflower diet diet ($\chi^2_1 = 1.233$, $p>0.1$) or the oats diet ($\chi^2_1 = 0.0741$, $p>0.1$). Litter sizes were not significantly different between the three seed diets, but the pellet fed mice had significantly larger litters than the seed fed mice ($F_{1,47} = 4.44$, $p<0.05$).

Conclusions

This experiment confirmed that rice is a poor-quality diet for breeding, relative to the other seeds, and to pellets. Although protein was the most likely limiting nutrient, other nutrients present in oats and sunflower, such as minerals, fatty acids and vitamins may have contributed to the improved breeding performance.

4.4. DISCUSSION

These experiments demonstrate clearly that a diet of pure rice is inadequate to support breeding in house mice. Mice fed pure rice usually did not breed, or produced only a single, small litter. Diets had little effect on body weight in any experiment. Pryor and Bronson (1981) also found diets which suppressed reproduction caused only a 1-2% loss in body weight. Therefore, it is unlikely that changes in weight were responsible for the changes in breeding performance. Natural supplements added to the rice diet, caused little improvement in breeding performance. Breeding performance improved only when supplements of rice sprouts were given, but sprout supplemented diets were still inferior to pellet diets. Breeding performance did not improve significantly when rice diets were supplemented with mealworms. Similarly, Pryor and Bronson (1981) found that when wheat grain or rye grass seed diets were supplemented with mealworms, there was no improvement in breeding performance. These findings suggest that the small amount of invertebrate tissue that mice include in their natural diet in rice stubble fields would probably be insufficient to make the diet adequate for breeding. Breeding performance also did not improve significantly when rice diets were supplemented with milk-ripe seeds. This is inter-

preted as evidence against the presence of a chemical in these seeds that stimulates breeding.

Protein was the only nutrient supplement to rice diets which significantly improved litter sizes and breeding intensity. The suppressive effects of inadequate dietary protein on endocrine activity and the functioning of the reproductive organs has been discussed in Section 1.1. Both the growth of the embryos and the production of milk require large amounts of protein. Payne and Wheeler (1968) estimated that non-primate diets suitable for lactation need to have a utilizable protein content more than double that required for maintenance. It is clear that rice does not contain sufficient protein to meet the demands of reproduction, and while a few females may have sufficient body stores to allow them to produce and wean a small litter after being put on a rice diet, most are unable to do so, and no females on a pure rice diet in any experiment were able to produce a second litter.

Breeding performance did not improve when a GA_3 supplement was added to a rice/casein/vitamin A diet. Mice on the control diet did, however, have large litter sizes and a high breeding intensity , so there was little room for improvement. While this result does not refute the conclusions of Olsen (1981), suggesting that GA_3 has a stimulatory effect on mouse breeding, it does indicate that a dietary source of GA_3 is not necessary for successful breeding.

The breeding performance of mice fed rice diets was not improved by a vitamin A supplement. Although it is well documented that mice fed a diet deficient in vitamin A will eventually become infertile (Wolfe and Salter 1931; Green 1970), McCarthy and Cereçedo (1952) found it much harder to produce vitamin A deficiency in three strains of albino mice, than in laboratory

rats. Hence they suggest that mice may be able to store considerable quantities of vitamin A in their bodies, or alternatively be economical in their use of it. They found that young albino laboratory mice receive vitamin A during lactation, and that this source is critical with respect to their future ability to withstand a sustained deprivation of dietary vitamin A initiated at weaning. In an experiment where mothers were given diets with adequate vitamin A, the young developed normally to adulthood even when fed vitamin A deficient diets after weaning, and on reaching sexual maturity the females gave birth to apparently normal litters. Control mothers, deprived of vitamin A from the 11th day of lactation onwards, had young that did not develop normally and were infertile. This ability to pass vitamin A on to the offspring, suggests that a deficient diet might need to be eaten by more than one generation before the deficiency would be severe enough to cause reproduction to cease. The ability to withstand a prolonged vitamin A deprivation could be an advantage to mice eating a predominantly cereal grain diet, as such food contains negligigible quantities of vitamin A. Pryor and Bronson (1981) also found mice could breed well on a diet of pure wheat grain, which would also contain negligible quantities of vitamin A. These findings do not support the proposals of Ward (1981) and Redhead (1982) that an undersupply of vitamin A in the diet might be a causal factor in the autumn-winter cessation of breeding of house mice in the field, but in contrast, suggest that house mice may be well adapted to breeding on vitamin A deficient diets. As mice have lived in man's grain stores and grain fields for many thousands of years, where their grain diets have probably been low in vitamin A, the evolution of such an adaptation has obvious advantages.

The finding that protein was the limiting nutrient in rice diets for breeding, suggested that supplementing the food supply of mice in rice stubble fields in autumn with a protein-rich

food, should improve their breeding performance. The results of Experiment 8, indicated that a mixture of oat grain and sunflower seeds would be a suitable dietary supplement to use in the subsequent field experiment designed to test whether an undersupply of dietary protein limits the breeing of mice in rice stubble fields.

Table 4.1. The influence of the protein content of the diet on two reproductive parameters of house mice.
N = mean number of litters born per female
L = mean litter size
NxL = mean number of young born per female
Where a given protein concentration in the first column, is marked (N), (L), or (NxL), then mice given the diet with that protein concentration showed a breeding performance in that reproductive parameter increased by >10% over mice given other unmarked diets in the same study. Where a study is shown to have monitored the reproductive parameters N,L or NxL, but no diets are marked for that study, then there was <10% difference between diet groups for that parameter.

Protein content of diet%	Mean number of pairs per diet	Parameter tested	Strain of mice	Reference
20 vs 24(N,L)	16	N,L	Albino	Cerecedo & Vinson (1944)
13.6(N) vs 15.0	22	N,L	Albino	Bruce and Parkes (1949)
15.0(L) vs 18.4	32	N,L	Albino	" " "
12.3(NxL) vs 14.7(NxL) vs 19.2	22	NxL	W-Swiss	Howie and Porter (1950)
4(N) vs 8(N) vs 23	7	N	C3H	Lee, King & Visscher (1952)
12.8 vs 20.2(N,L)	50	N,L	white standard	DeMeillon & Paterson (1958)
9.4 vs 11.4 vs 13.6 vs 16.3	25	L	Swiss STM	Goettsch (1960)

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Table 4.1. Continued.

Protein content of diet%	Mean number of pairs per diet	Parameter tested	Strain of mice	Reference
17.0(N,L) vs 25.0	300	N,L	DBA/2J	Hoag and Dickie (1960)
17.0(N,L) vs 25.0	328	N,L	C57BL/6J	" " "
17.0 vs 20.0(N)	56	N,L	C57BL/6J	Hoag and Dickie (1962)
20.0(N) vs 22.0 vs 24.0	56	N,L	AKR/J	" " "
20.0 vs 22.0 vs 24.0	56	N,L	DBA/2J	" " "
18.0 vs 24.0	143	N,L	4 inbred strains	Knapka *et al.* (1977)

Table 4.2. The dietary concentrations of seven minerals required by mice for reproduction* and the concentrations of these minerals in husked rice**

Mineral	Husked rice mg/kg	Minimum dietary requirements mg/kg
Copper	3	16
Manganese	56	104
Iron	32	255
Calcium	927	4000
Phosphorus	3930	4000
Potassium	1421	2000
Magnesium	778	500

* National Research Council (1978)
** Grist (1970)

Table 4.3. Ages and body weights of experimental mice on the day feeding treatments started. Ages were only known for experiments in which laboratory born mice were used.

Experiment number	Age range (weeks)	Male weight range (g)	Female weight range (g)
1	8 - 14	11.7 - 19.6	10.0 - 18.4
2	6 - 16	11.5 - 24.5	8.7 - 19.3
3	7 - 13	-	10.0 - 15.0
5	9 - 14	15.0 - 20.7	10.0 - 17.9
8	3 - 6	4.0 - 11.6	4.2 - 9.5

Table 4.4. Body weights of mice in Experiment 1. There were 11 pairs of mice on each feeding treatment. All means are given with one standard error. By day 5 of the treatment, all mice given the wheat plant diet had either died or were so weak they were given an alternative food.

Day of treatment	Barley grass seed		Wheat plants	
	Males	Females	Males	Females
Day 0	15.2±0.7	12.5±0.7	15.1±0.7	12.7±0.8
Day 3	13.7±0.6	11.8±0.6	12.0±0.6	10.4±0.6
Day 10	13.8±0.5	12.2±0.6	-	-
Day 20	14.6±0.5	13.2±0.6	-	-

Table 4.5. Results of Experiment 2. There were 18 pairs of mice on each feeding treatment. All means are given with one standard error.

Day number		Pellets		pellets plus milk-ripe wheat	
		Males	Females	Males	Females
0	Mean weight (g)	17.3±1.0	12.5±0.6	17.1±1.0	13.0±0.7
42	Mean weight (g)	19.4±0.9	–	18.6±0.8	–
42	Mean testes weight (g)	0.16±0.01	–	0.16±0.01	–
by 42	Number of first litters born		9		5
42	Number pregnant at autopsy		4		3
by 42	Number pregnant or lactating		13		8
by 42	Mean first litter size		5.5±0.4		5.4±0.2

Table 4.6. Results of Experiment 3. There were 11 females on each feeding treatment. All means are given with one standard error.

Day of treatment		Mature rice grain	Milk-ripe rice grain
0	Mean body weight (g)	12.0 ± 0.4	12.3 ± 0.5
9	Mean body weight (g)	12.7 ± 0.4	12.7 ± 0.5
9	Mean uterine weight (mg)	159 ± 25	152 ± 38
9	Mean paired ovarian weight (mg)	29.1 ± 3.3	23.6 ± 1.8

Table 4.7. Results of Experiment 4. There were twelve pairs of mice on each feeding treatment. All means are given with one standard error.

Day number		Rice	Rice and sprouts	Rice and mealworms	Rice and sprouts and mealworms	Pellets
0	Mean male weight (g)	16.7±0.5	16.8±0.5	16.8±0.5	16.8±0.5	16.9±0.6
0	Mean female weight (g)	12.3±0.5	12.3±0.5	12.3±0.4	12.4±0.5	12.5±0.5
109	Mean male weight (g)	16.1±0.5	15.8±0.3	16.8±0.8	17.1±0.3	17.6±0.6
by 109	Number of first litters	0	6	5	6	6
by 109	Mean first litter size at birth	-	4.3±0.7	4.4±0.2	4.2±0.3	5.3±0.8

Table 4.8. Results of Experiment 5. There were eight pairs of mice on each feeding treatment. All means are given with one standard error.

Day number	Diet	Pellets	Pellets plus sprouts	Rice	Rice plus sprouts
0	Mean female weight (g)	13.5±0.7	13.1±0.7	13.2±0.7	13.7±0.8
0	Mean male weight (g)	17.5±0.6	17.1±0.5	17.1±0.4	17.3±0.5
40	Mean female weight (g)	13.4±1.4	14.4±0.5	14.0±0.7	15.3±0.8
40	Mean male weight (g)	16.6±0.4	16.9±0.4	16.6±0.3	16.9±0.4
by 140	Number of first litters	8	7	3	7
by 140	Mean first litter size at birth	4.9±0.3	4.9±0.4	3.0±0.6	3.9±0.5
by 140	Number of second litters	6	6	0	3
by 140	Mean second litter size at birth	5.7±0.4	5.3±0.6	-	3.3±0.9
by 140	Number of third litters	5	4	0	1
by 140	Mean third litter size at birth	6.6±0.5	5.8±0.6	-	4.0

Table 4.9a. Results of Experiment 6. There were 22 pairs of mice on each feeding treatment. All means are given with one standard error.

Day number	Diet	Rice	Rice + casein	Rice + vitamin-A	Rice + casein + vitamin-A	Rice + GA3 + casein + vitamin-A
0	Mean female weight (g)	16.4±0.6	16.3±0.6	16.4±0.6	16.4±0.6	16.4±0.6
0	Mean male weight (g)	17.2±0.6	17.2±0.7	17.2±0.6	17.1±0.6	17.1±0.6
30	Mean female weight (g)	15.7±0.5	16.8±0.5	16.0±0.6	16.3±0.4	16.3±0.5
30	Mean male weight (g)	16.6±0.4	16.9±0.6	16.1±0.5	16.5±0.4	16.7±0.5
by 90	Number of first litters	7	17	11	12	15
by 90	Mean first litter size at birth	3.7±0.4	5.5±0.3	4.4±0.3	5.8±0.3	5.1±0.3
by 110	Mean first litter size at weaning	3.1±0.3	4.9±0.4	3.6±0.3	4.8±0.5	4.2±0.5

Table 4.9b. Analysis of breeding data from Experiment 6. Values are differences in deviance for breeding intensity, and variance ratios for litter sizes. Degrees of freedom are given in brackets.

Source	Casein	Vitamin A	Vitamin A x casein	GA_3
Breeding intensity	7.072** (1)	0.0188 (1)	3.229 (1)	0.460 (1)
Mean first litter size at birth	18.29*** (1,44)	1.67 (1,45)	0.15 (1,43)	0.95 (1,31)
Mean first litter size at weaning	22.90*** (1,44)	1.49 (1,45)	0.03 (1,43)	1.26 (1,31)

* $p<0.05$
** $p<0.01$
*** $p<0.001$

For method of analysis for breeding intensity see Appendix 2g.
For method of analysis for litter size see Appendix 2e.

Table 4.10a. Results of Experiment 7. There were 23 pairs of mice on each feeding treatment. All means are given with one standard error.

Day number	Diet	Rice	Rice + mealworms	Rice + milk-ripe rice	Rice + mealworms + milk-ripe rice
0	Female weight (g)	16.5±0.5	16.4±0.6	16.6±0.6	6.5±0.6
0	Male weight (g)	17.2±0.6	17.0±0.6	17.0±0.6	17.0±0.6
30	Female weight (g)	15.9±0.5	16.4±0.6	15.8±0.4	16.5±0.6
30	Male weight (g)	16.6±0.4	16.8±0.5	16.5±0.6	16.5±0.5
by 90	Number of first litters	7	11	8	11
by 90	First litter size at birth	3.7±0.4	4.5±0.5	4.1±0.5	4.2±0.3
by 110	First litter size at weaning	3.1±0.3	3.9±0.4	3.4±0.7	3.9±0.3

Table 4.10b. Analysis of breeding data from Experiment 7. Values are differences in deviance for breeding intensity, and variance ratios for litter sizes. Degrees of freedom are given in brackets.

Source	Mealworms	Milk-ripe rice	Mealworms x milk-ripe rice
Breeding intensity	2.227 (1)	0.0463 (1)	0.053 (1)
Mean first litter size at birth	0.90 (1,34)	0.00 (1,35)	0.71 (1,33)
Mean first litter size at weaning	3.713 (1,34)	0.081 (1,35)	0.120 (1,33)

For method of analysis of breeding intensity see Appendix 2g.
For method of analysis of litter sizes see Appendix 2e.

Table 4.11. Results of Experiment 8. There were 27 pairs of mice on each feeding treatment. All means are given with one standard error.

Day number	Diet	Rice	Oats	Sunflower and oats	Pellets
0	Mean female weight (g)	6.6±0.3	6.7±0.2	6.7±0.2	6.7±0.2
0	Mean male weight (g)	7.6±0.4	7.5±0.4	7.4±0.3	7.3±0.3
0	Number of perforate vaginae	0	0	0	0
60	Mean female weight (g)	9.9±0.3	9.8±0.3	10.1±0.3	10.2±0.3
60	Mean male weight (g)	12.6±0.3	11.7±0.3	12.6±0.3	14.2±0.4
70	Number of perforate vaginae	9	16	18	17
122	Mean male weight (g)	13.9±0.3	13.4±0.3	14.1±0.4	15.5±0.4
by 137	Number of first litters	4	13	18	14
by 137	Mean first litter size at birth	3.8±0.3	3.6±0.4	3.7±0.4	4.6±0.3

CHAPTER FIVE

A FIELD EXPERIMENT TO EXAMINE THE EFFECT OF FOOD QUALITY ON THE CESSATION OF BREEDING

5.1. INTRODUCTION

In Chapter Two it is suggested that the decline in breeding intensity in rice stubble fields in autumn, is a response to the poor-quality diet. In rice fields the diet contained more than 95% mature rice grain from the end of March to the end of July (Figure 2.6a,c) and over this period breeding ceased. The experiments on caged mice described in Chapter Four suggest that protein is the limiting nutrient for reproduction in mice fed a diet of mature rice grain. In an experiment where rice was supplemented with protein (casein), breeding performance (litter size, and numbers of females breeding) was significantly improved (Table 4.9b). It is therefore proposed that a lack of protein in the diet limits the breeding of mice in rice stubble fields in autumn. If this is true, then experimentally increasing the protein content of the diet of mice in the field by supplementary feeding should improve their breeding performance.

That low-quality food is a cause of the autumn decline in reproductive performance of mice in rice stubble fields has previously been proposed by Redhead (1982). He also suggests that the lowered reproductive condition of mice is associated with reduced efficacy of spacing behaviour, which allows more juveniles to be retained in the population, so the population density increases, which in turn acts to further suppress breeding. He developed a 'spacing behaviour - food quality' hypothesis to describe these events. The following quote from Redhead's thesis summarizes his hypothesis:

'Some dietary component, perhaps vitamin A or its precursors, or a phyto-oestrogen, becomes less available as the cereal crops ripen. The reduced availability reduces the fertility of adult males and females, and delays the onset of puberty in juveniles. The reduction in fertility is not complete, however, and some reproduction may still occur. In their pre-pubertal condition, juveniles are not affected by the territorial marking pheromones (which may also be of reduced efficacy because of their testosterone-dependence) and therefore feel no imperative to disperse. The population density increases and the male/female mutual stimulation process is consequently disrupted, so that the regression of previously sexual adults becomes complete.'



Redhead (pers. comm.) considers that this hypothesis falls within the general 'unifying' theory proposed by Tamarin (1983) that states 'All animal populations are regulated ultimately by a limiting resource(s), such as food, and proximately by their social behaviour and organization'. Tamarin believes that 'there is strong empirical evidence for the role of social behavior in inhibiting reproduction and limiting population density of breeding individuals from studies of confined rodent populations'. Hence he thinks that there can be an interaction between nutrition and behaviour, and that both may act together to limit breeding and population density.

Redhead did not analyse the diet of mice, but he discussed three possible 'dietary components' that might be limiting for reproduction. These were:

i). *Protein.* He thought protein was unlikely to be limiting

reproduction: 'While rice is deficient in protein . . . enough other sources of protein were available to provide a suitably balanced diet for reproduction'.

ii). *Phyto-oestrogens and other fertility agents.* He cites references that show mice are able to breed on a diet of pure dried cereal and concludes from this evidence that phyto-oestrogens alone are unlikely to be responsible for any observed decline in breeding of mice eating such a diet in the field.

iii). *Vitamin A.* He thinks vitamin A (or its precursors) are likely to be limiting: 'Vitamin A therefore remains a likely candidate as the external factor determining the onset and cessation of breeding'. Ward (1981) had previously suggested this vitamin might limit the breeding of wild mice.

The experimental results and literature reviewed in Chapter Four, however, suggest that protein is probably the limiting nutrient, and that the additional sources of protein that mice include in their diet, such as small quantities of dicotyledon seeds and invertebrates, are unlikely to make good the deficiency. There is also evidence presented in Chapter Four that a lack of fertility agents and vitamin A in the diet of mice has little short-term effect on their breeding performance.

In view of this proposed combined effect of both decline in food quality and the social factors associated with an increase in population density, as a cause of the decline in breeding, an experiment designed to test the effects of food quality alone might have given misleading results. So the experiment described in this chapter was designed to test the effects of both food quality, population density and their combined effect on breeding performance. If the retention of juveniles in the population and the consequent increase in population density is responsible for

the suppression of the fertility of adults, as suggested by Redhead, then the experimental culling of juveniles should reverse this process. If the poor diet quality is responsible, then experimental improvement of the diet by supplementary feeding should reverse the process. If it is the interaction between these two factors, then both treatments combined should be effective.

HYPOTHESIS: A decline in food quality, associated with an increase in population density, causes a decline in breeding intensity in rice stubble fields in autumn.

The following experimental design was used to test the hypothesis. Two factors, each set at two levels in a 2^2 factorial design constituted the experimental treatments:

Factor 1 = food quality:
S = high quality (protein supplemented diet)
R = low quality (natural rice diet).
Factor 2 = population density:
N = high density (natural population density)
C = low density (juveniles culled from population).

This gave four treatment combinations: SN, SC, RN and RC.

5.2. METHODS

5.2.1. Study Site

In the selection of a study site for this experiment, an attempt was made to meet these conditions:

1. An area of at least 40 ha.

2. A rice crop that would be harvested by early April.
3. Contour banks sufficiently widely spaced so that experimental grids could be spaced fairly evenly across the field.
4. A density and distribution of mice suitable for the imposition of experimental treatments.

In early 1983 there was a shortage of irrigation water owing to a severe two-year drought. Farmers had to reduce the area sown to rice, and it was not possible to find a sufficiently large rice crop to meet Condition 1. Two rice crops on neighbouring farms were therefore combined as study sites; Farm 1061 (Farm 1) with 20 ha sown to pelde rice, and Farm 1057 (Farm 2) with 20 ha sown to calrose rice; both in the Warrawidgee district of the MIA. Both farmers expected to harvest the rice by early April, which fulfilled Condition 2. The spacing of banks on these two farms met Condition 3. Preliminary trapping at random locations in these fields in January 1983, gave a trap success above 30% at all sites, indicating that the density and distribution of mice met condition 4 adequately.

Maps of the two study sites, drawn from aerial photographs, are presented in Figure 5.1. They show the position of the contour banks, the sites of the experimental grids, and the land use in the neighbouring fields.

Temperature and rainfall data for the experimental period are presented in Figure 5.2. Temperatures were close to the average for the time of year. The years 1981 and 1982 were drought years, but the drought broke in late March 1983, just as the experiment started.

On 20 March, just before the first trap-session, the rice crops on both farms were at the dough-ripe stage (between milk-ripe and maturity). The irrigation water was being drained from

the rice bays at this time, and a harvest completed by mid-April was forcast. But heavy rains fell between 20 and 30 March and delayed draining, and many bays were still flooded on 30 March. The rainfall in April and May 1983 was more than double the average, and more than five times the April-May rainfall in 1982. This caused repeated flooding of the rice bays. The ground remained too soft for the harvesting machines, and the rice on Farm 2 was not harvested until 18 - 22 May, just before the fourth trap-session, and the rice on Farm 1 was not harvested until 16 - 20 June, just after the final trap-session. So the experiment was conducted in rice crops, rather than in stubble, as intended. As soon as the harvest was completed on Farm 2, wire sheep fences were erected around the experimental grids, two metres out from the perimeter trap sites (Figure 5.3). The experiment continued for only three weeks after the sheep were put into the field, so they did not have much effect on the condition of the stubble. Sheep fences were not needed on Farm 1 because of the late harvest.

The contour banks on both farms supported a moderate weed growth (Figure 5.3). On Farm 1, sheep had been temporarily put out to graze on the contour banks during January and February and this had slightly reduced the weed cover on its banks. Grass species on all contour banks were patchy in distribution. Barnyard grass was the most common species and it continued to set seed in the early weeks of the experiment. Couch grass and paspalum also seeded, but these seeds are not thought to be eaten by mice (Table 2.5). The contour banks also supported a patchy distribution of dicotyledons, mainly blackberry nightshade, which produced fruits over the duration of the experiment, and saffron thistle, which seeded in March and April. No weeds produced seeds in the rice bays.

5.2.2. Layout of grids

The experiment was conducted in two rice fields with eight grids in each field (Figure 5.1). Each grid contained forty-five feeders, set out in five rows of nine. The centre row was placed along a fairly straight section of contour bank, and two rows were spaced out 8 m apart parallel to the bank on each side. The nine feeders in each row were also spaced at 8 m intervals. Grids were spaced as evenly as possible across the fields. The minimum distance between the edges of two adjacent grids was 65 m. Each of the four treatments (SC, SN, RC and RN) were replicated twice on each farm, giving a total of four replicates of each treatment. Allocation of treatments to individual grids was random.

5.2.3. Population monitoring

Trapping on grids was conducted in five trap-sessions: one before treatments started (pre-treatment trap-session T1, 29 Mar. - 7 Apr.) and during the treatments (treatment trap-sessions T2, 15 - 24 Apr.; T3, 6 - 13 May; T4, 21 - 28 May; T5, 9 - 18 June). A single Longworth trap was set at each feeder site, 45 to each grid. In each trap-session the traps were set for three successive nights. As the daylength was too short to process mice from more than eight grids in a single day, and as there were insufficient traps to trap on all grids simultaneously, Farm 1 was trapped for the first three nights of each trap-session, followed by Farm 2. Traps were baited with calrose rice, and feeders were kept filled with the normal food on trap nights. Mice were scored for reproductive condition, body weight and length by the same methods as in the previous experiment (Section 3.2.3). Mice scored as 'breeding' were either pregnant or lactating.

To check if the method of trapping had adequately sampled the mouse populations on the grids, and also to check if placing traps at feeder sites had caused any bias in favour of catching breeding females, 90 longworth traps, twice the usual number, were set out on two high-quality food grids on Farm 2, on 18 June, two days after the final trap-session. Half the traps were set at feeder sites, and half in positions half way between feeder sites. The results of this trapping are presented in Table 5.1. The traps placed at the intermediate sites caught just as high a proportion of tagged recaptures as the traps at the usual feeder sites so it was concluded that the traps had been close enough in normal trapping to adequately sample the population. Further, there was no indication of a difference in the proportion of breeding females between the feeder trap-sites and the half-way trap-sites.

5.2.4. Supplementary feeding

Food quality was set at high (S) and low (R) levels.
S. high = sunflower seeds and oat grain mixed in equal quantities, provided as a supplementary food. This mixture was chosen because 1) these seeds are high in protein, 2) they are attractive to mice and 3) they support a good breeding performance in caged mice (Section 4.3, Experiment 8).
R. low = rice grain provided as a supplementary food. Rice grain was the staple food of mice in this habitat at this time of year (Figure 2.6a,e), and caged mice fed a diet of pure rice had been shown to breed poorly (Section 4.3).

A single 375 ml aluminium beer can, half open at one end and placed on its side (Figure 5.4) was placed at each feeder site. These cans were kept half full of the supplementary food which was checked daily, and replaced if it was eaten or wet. When the

oats and sunflower seeds were first put out, only small quantities were eaten by mice. By the second week, however, nearly all feeders were being visited, and both types of seed were being eaten. The mice scattered a lot of seed and when the bays flooded more was washed out of the feeders. This made it impossible to obtain reliable estimates of the average consumption rates of seeds by the mice. Over the duration of the experiment, 150 kg each of oats and sunflower seeds were put out on the grids but much of this was not eaten. Some of the oats and sunflower seed scattered around the feeders started to germinate in mid-April, and further seed germinated throughout the experiment (Figure 5.4). This germinating seed was eaten by mice, especially the dicotyledon and embryo tissue of newly germinated seeds.

Mice ate much less seed from the rice feeders, but this was expected, as there was an abundance of rice grain available on all grids (Figure 5.5). Even so, most rice feeders had to be refilled about once a week. Both unharvested rice, and rice spilt from the feeders germinated during the experiment.

5.2.5. Culling

Population density was set at high (N) and low (C) levels.

N. high = natural density: Preliminary trapping for one night in January on contour banks showed there was a moderately high density of mice on both farms. This, together with Redhead's (1982) findings on seasonal trends in mouse population densities, suggested that the density of mice would be high and increasing over the experimental period.

C. low = culled density: Juvenile mice were culled from grids in all five trap-sessions. The minimum head-body length at which pregnant females had been observed frequently in previous trapping by Redhead (pers. comm.) was 75 mm, so this was arbitrarily

chosen as the cut-off point. All females ≤75 mm caught during the treatment trap-sessions were culled. In caged-reared mice of known age, males averaged 82 mm in length when they were the same age as females of 75 mm, so all males ≤82 mm caught were also culled. A total of 420 small mice were culled during the experiment, which is an average of 13 mice on each culling grid in each trap-session. Thirteen mice was, on average, 38% of all mice captured.

5.2.6. Diet analysis

Snap-traps were set on the nights of 17 and 18 June (after T5), at feeder sites on some grids on both farms. The stomachs were removed from 46 mice from high-quality food grids and 20 from low-quality food grids. These were preserved in 70% ethanol and the contents later identified and quantified by the method described in Section 2.2.5). This gave data for the mean percentage by volume of each food type present in the stomachs. These values were converted into mean percentages by dry weight to allow estimations of protein content ~~to~~ be made. Conversion factors were obtained by the following method. For seeds, ten grams dry weight of rice, oats and sunflower seeds were soaked in water for 12 hours; the soaked seeds were then blotted dry and their volume to the nearest millilitre was measured by displacement of water in a graduated glass tube. For insects and for non-seed plant material, the volume of samples of live mealworms and fresh green plant material were measured by water displacement, and then these samples were dried to constant weight and their dry weight recorded. The wet volume in millilitres of 10 g dry weight of each of these five food types are: rice = 12 ml, oats = 13 ml, sunflower = 14 ml, mealworms = 36 ml and plant material = 62 ml. These volume-to-weight ratios were used to convert the mean percentage volume of food types in the stomach

contents, to estimates of mean percentage dry weight.

Samples of husked and dried rice, oats, sunflower seeds and mealworms were analysed for protein content by the method described in Section 2.2.8. Protein contents of non-seed plant tissue, which was mainly leaf material, and for unidentified dicotyledon seeds, were obtained by taking the mean values for percentage protein of foods in these categories in tables published by the Food and Agriculture Organization (1970). The estimated mean percentage of each food type by dry weight in the stomachs, together with the estimated protein contents of these foods, was used to calculate the estim-ated percentage protein in the diets of mice on high-quality and low-quality feeding grids.

5.2.7. Data Analysis

The data unit was the number of mice caught per grid in each trap session (n), or subsets of this unit. The same parameters as those described for the first field experiment (Section 3.2.4.) were analysed for treatment effects and the same symbols were used for these parame-ters. The analysis was restricted to between-treatments within-trap-sessions for the reasons given in Section 3.2.4.

Farms were assumed to be a random variable, and therefore the farm effect was not expected to show a significant interaction with any of the other treatment effects. This assumption was tested for all four population parameters in all trap-sessions and was found to hold true, except for two data sets from trap-session T4, where the data for the total numbers of females caught, and the proportion of adult females breeding both showed a significant interaction between treatment and farm effects ($p<0.05$). These isolated occurrences of significant interac-

tions, in two out of the forty tests, were thought not to invalidate any of the conclusions drawn from the results described in this chapter.

Two-way analysis of variance tests were conducted to test for treatment effects on the numbers of mice caught on grids (parameters n,f,m and h). These data sets were found to have approximately normal distributions, so analyses were conducted on untransformed data. The sources of variation and associated degrees of freedom are presented in Table 5.2. This analysis was facilitated by use of the program GENSTAT (Rothamstead Experimental Station 1977), and an example of an analysis program is presented in Appendix 2f.

To determine if treatments affected on-site survival of females, instantaneous rates of decline (IRD) were calculated (Andrewartha and Birch 1954), based on the recapture rate of females originally ear-tagged and released in the first trap-session T1:

$$IRD = \frac{\ln(F_T+0.5/F_{T+1}+0.5)}{D}$$

F_T = number of tagged females (originally captured in T1) released in a trap-session T

F_{T+1} = number of tagged females re-captured in the following trap-session T+1

D = number of days between T and T+1.

IRD values were calculated independently for each of the sixteen grids, on each of the four intervals between trap-sessions (periods (P1 to P4). These IRD data set was tested for significant treatment effects with a three-way analysis of variance. Sources of variation and associated degrees of freedom for this test are

presented in Tab

Logistic regression analyses (Section 3.2.4.) were conducted to test for treatment effects on data in the form of proportions (parameters F,T,P and B). This analysis was again facilitated by use of the program GENSTAT, and an example is presented in Appendix 2g.

To determine if treatments affected condition indices, data for males was analysed for each trap-session. Males from grids on the same farm receiving the same experimental treatment were pooled, giving a total of eight samples from each trap-session. For each sample values of ln W were regressed on ln L and the eight regression lines were compared for differences in slope, using the method described previously (Section 3.2.4), following Redhead (1982). In trap-sessions where slopes for these eight lines were found not to differ significantly, an analysis of covariance was then conducted, with ln L as the co-variate, to test for effects due to farm, food, culling or food x culling on the condition index ln W.

5.3. DESCRIPTION OF POPULATIONS

5.3.1. Total numbers

The data for the number of mice (n) caught per grid in each trap-session are given in Table 5.5a. Mean values of mouse numbers for each trap-session for Farm 1 versus Farm 2 grids, for high-quality food grids versus low-quality food grids, and for culled versus unculled grids, are presented in Figure 5.6a,b,c respectively. The results of the analysis of these data for treatment effects in each trap-session are presented in Table 5.5b. In T1 there were no significant differences in population

presented in Table 5.3.

Logistic regression analyses (Section 3.2.4.) were conducted to test for treatment effects on data in the form of proportions (parameters F,T,P and B). This analysis was again facilitated by use of the program GENSTAT, and an example is presented in Appendix 2g.

To determine if treatments affected condition indices, data for males was analysed for each trap-session. Males from grids on the same farm receiving the same experimental treatment were pooled, giving a total of eight samples from each trap-session. For each sample values of ln W were regressed on ln L and the eight regression lines were compared for differences in slope, using the method described previously (Section 3.2.4), following Redhead (1982). In trap-sessions where slopes for these eight lines were found not to differ significantly, an analysis of covariance was then conducted, with ln L as the co-variate, to test for effects due to farm, food, culling or food x culling on the condition index ln W.

5.3. DESCRIPTION OF POPULATIONS

5.3.1. Total numbers

The data for the number of mice (n) caught per grid in each trap-session are given in Table 5.5a. Mean values of mouse numbers for each trap-session for Farm 1 versus Farm 2 grids, for high-quality food grids versus low-quality food grids, and for culled versus unculled grids, are presented in Figure 5.6a,b,c respectively. The results of the analysis of these data for treatment effects in each trap-session are presented in Table 5.5b. In T1 there were no significant differences in population

density between farms or between grids allocated to different experimental treatments. There were more mice on Farm 1 than on Farm 2 in all five trap-sessions, and this difference was significant in T2, T3 and T4. There were more mice caught on high-quality food grids than on low-quality food grids in all four treatment trap-sessions, and this difference was significant in T2, T4 and T5. The culling treatment failed to have a discernable effect on population density even though 420 mice were removed from culling grids over the duration of the experiment. There was no significant interaction between food-quality and culling in any trap-session.

5.3.2. Numbers of adult females

The data for the number of adult females (f) caught per grid in each trap-session are presented in Table 5.6a. The shortest head-body length at which a female was recorded as being pregnant in the present experiment was 80 mm, so all females ≥ 80 mm were classified as adults. Mean values for numbers of adult females compared for farm, food quality and culling are presented in Figure 5.7a,b,c respectively. The results of the analysis of the data on adult female numbers for treatment effects are presented in Table 5.6b. Adult female numbers showed the same general treatment effects as total mouse numbers. There were significantly more females on Farm 1 than on Farm 2 in all five trap-sessions. There were more adult females on high-quality food grids than on low-quality food grids in all four treatment trap-sessions, and this difference was significant in T3 and T4. Culling had no discernable effect on adult female numbers and there were no significant differences between culled and unculled grids in any trap-session. There were no significant interactions between food-quality and culling in any trap-session.

A further analysis was conducted on the proportion of adult females in the total numbers of mice caught per grid (f/n) in each trap-session. Mean fitted values of these proportions for comparisons by farm, food-quality and culling treatments, are presented in Figure 5.8a,b,c respectively. The results of the analysis of these data for treatment effects are presented in Table 5.6c. There were significant effects only in T1, when Farm 1 had a significantly higher proportion of female mice than Farm 2; in T3, when the proportion of adult females in the total catch was significantly higher on high-quality food grids than on low-quality food grids; and in T5, where there was a significant positive interaction between food quality and culling.

5.3.3. Recaptures

Data for the numbers of tagged mice that were recaptured from previous trap-sessions (m) are presented in Table 5.7a. and the results of the analysis of these data for treatment effects in Table 5.7b. The only significant differences in the proportion of mice that were recaptured were in T2, when there was a significantly higher proportion of recaptured mice caught on high-quality food grids than low-quality food grids.

Data for the numbers of adult female mice caught on grids that were recaptured from previous trap-sessions (h) are presented in Table 5.8a. The data for the proportion of recaptured females in the total number of adult females caught per grid (h/f) were analysed for treatment effects and the results of this analysis are presented in Table 5.8b. Significant effects were found only in T2, when there was a higher proportion of females that were recaptures on Farm 1 than on Farm 2; and in T5, when there were a higher proportion of adult females that were recaptures on unculled grids than on culled grids.

Values for instantaneous rates of decline (IRD) were calculated for females, based on the recapture rate of females originally tagged in the first trap-session T1. The data for these IRD values is presented in Appendix 3. Analysis of variance tests on the IRD values for treatment effects yielded no significant differences due to any of the treatments tested (Table 5.3, $p>0.05$ for all tests). Hence, there was no evidence to suggest that treatment had any effect on retention periods for females on grids.

5.3.4. Movements

A total of 452 mice were recaptured one or more times and 178 of these were females (39.4%). Of these recaptured mice, only 19 (4.2%) had changed grids betwen captures (6 females, 13 males). Nine of the mice had moved to high-quality food grids and ten to low-quality food grids, and seven had moved to culled grids and twelve to unculled grids. There was therefore no indication that the direction of movement was affected by the experimental treatments.

5.4. RESULTS

5.4.1. Diet

The percentage volumes and estimated percentage dry weights of the food types identified in the stomachs of mice caught in break-back traps on high-quality and low-quality food grids after T5 are presented in Table 5.4 . The protein content of the main food types are also presented in this table, together with estimates of the protein content of the stomach contents of mice

under the two feeding treatments. From these values it is estimated that mice on high-quality food grids had, on average, 3.3% more protein in their diet than mice on low-quality food grids.

5.4.2. Breeding intensity

The data for the number of breeding females (r) caught per grid in each trap-session are presented in Table 5.9a. The proportion of breeding females in the total adult female catch (r/f) was taken as an index of breeding intensity, and mean fitted values for breeding intensity, compared for farm, food-quality and culling treatments are presented in Figure 5.9a,b,c.

Figure 5.9b shows that breeding intensity was initially around 70% on both high-quality and low-quality food grids. Breeding intensity then declined on low-quality food grids, and remained at around 40% for the remainder of the experiment, whereas on high-quality food grids, there was an initial decline, in trap-session T2, and then breeding intensity increased and remained around 65% for the final three trap-sessions.

The data for breeding intensity (r/f) were analysed for treatment effects and the results of this analysis are presented in Table 5.9b. There was a significantly higher breeding intensity on Farm 2 than on Farm 1 in T1, T4, and T5. There were no significant differences in breeding intensity due to food quality in T1 or T2, but there was a significantly higher breeding intensity on the high-quality food grids than on low-quality food grids in T3, T4 and T5 (Figure 5.8b), and these differences were highly significant ($p<0.01$, Table 5.9b). There were no significant differences in breeding intensity due to culling or food-quality x culling in any trap-session.

Litter sizes were recorded by autopsy from pregnant mice caught in break-back traps on 17 and 18 June. The mean litter size (± one standard error) of the 14 pregnant mice caught on high-quality food grids was 6.8±0.4, and of the 6 pregnant mice caught on low-quality food grids was 6.0±0.7. These mean litter sizes were clearly not significantly different.

5.4.3. Condition index

Data for males was analysed to see if treatment affected their condition index. Males receiving the same treatment on the same farm were pooled to give eight samples and ln W was regressed on ln L for each sample. The eight regression lines were tested for differences in slope, and the results of this analysis are presented in Table 5.10. A significant difference in slope was only found in T4. For these T4 data, the confidence intervals around the fitted values of ln W on the eight lines were calculated for the minimum, mean and maximum values of ln L in the data set. All the confidence intervals overlapped, so it was concluded that over the range of lengths included in the data set, there were no treatment effects on the weight-length relationship.

For the data from the other trap-sessions with parallel regression lines, it was possible to conduct an analysis of covariance, using ln L as the co-variate, to test for treatment effects on Ln W adjusted for length. The results of this analysis are presented in Table 5.11. In T1, T3 and T5 there were significant differences in ln W (adjusted for ln L) in mice from different farms. In T1 and T2 the interaction of food x culling was also significant. As T1 was the pre-treatment trap-session, however, these differences existed before the experimental treatments were applied, so there was no true indication of a food x

culling interaction. There were no main effects due to either the food or culling treatments in any trap-session.

5.4.4. Body fat

The carcasses of mice caught in break-back traps on grids on 17 and 18 June, after T5, were frozen and their body fat content was analysed (Section 2.2.7.). The mean percentage fat contents for mice from high-quality and low-quality food grids are presented in Table 5.12. It is clear that supplements of high-quality food did not affect body fat content.

5.5. DISCUSSION

The results of this experiment showed that food quality limited breeding intensity in rice fields in autumn. The provision of high-quality food reversed the decline in breeding intensity which usually occurs in rice fields in autumn (Figure 2.6a,c; Redhead 1982), and mice on experimental grids with a high-quality diet maintained their breeding intensity at around 65% in the final three trap-sessions, while the corresponding figure for control grids was around 40%. Therefore the null hypothesis, that breeding intensity of mice in autumn rice stubble fields is not affected by food quality, was rejected. This is the first time that food quality, as opposed to food abundance, has been demonstrated to affect breeding in a field population of house mice, though it has been demonstrated previously for natural populations of a couple of other rodents species (Negus and Berger 1977; Cole and Batzli 1978), and more frequently in birds (Moss *et al.* 1975; Jones and Ward 1976; Ewald and Rohwer 1982), and it is well documented that food quality affects the breeding performance of livestock (Lamond and Bindon 1969;

Elsey 1973).

The autumn of 1983 had more rainfall than usual, and this is believed to be the cause of the continuation of breeding on the grids which were not provided with supplementary high-quality food. Similarly, Redhead (1982) suggests that in 1977, when breeding continued through the winter on rice fields in his study area, the causal factor was high autumn-winter rainfall. He suggests that the rain prolonged the seeding of barnyard grass and that this high-quality food in the diet allowed breeding to continue. In the present study barnyard grass was not as abundant as in Redhead's study area, and it was not detected in the stomachs of mice caught on the experimental grids in late June. So, although 1983 had a wet autumn like 1977, some factor other than abundant grass seeds must have caused the prolongation of breeding on the control grids. One possibility not yet investigated in the field is that the inclusion of germinated grain in the diet is responsible for the continuation of breeding in wet years. Tests on caged mice (Section 4.3) show that while mice on a diet of mature rice grain breed poorly or not at all, only small supplements of germinated rice allow them to significantly improve their breeding performance. Germinated grain has a higher protein content than dry mature grain and a higher GA_3 content, and it is also richer in some vitamins (Section 4.1.). The method used for identifying food in the stomachs of mice in the present study, did not distinguish between endosperm eaten from germinated or ungerminated seeds. Germinated seeds were abundant in the study area, and many were observed that had been chewed by mice. Caged mice, given germinated and ungerminated rice, nearly always eat the endosperm from germinated rice in preference to ungerminated rice (pers. obs). So it is likely that mice in rice fields in wet autumns include enough germinated grain in their diet to enable them to continue breeding.

Culling did not affect either population density or breeding intensity. Therefore the null hypothesis, that breeding intensity is not affected by population density, was not tested. The reason why culling failed to reduce numbers is uncertain. Possibly the culling was not severe enough to remove a sufficient proportion of the total population to reduce trap-success, or new mice may have moved onto the culled grids to replace the mice that were removed. An alternative explanation, in accordance with Redhead's food-quality, spacing behaviour model, is that density was socially regulated, and young mice were being forced to disperse, so that on culling grids the removal of young mice only pre-empted their natural dispersal. Redhead suggested that social regulation of population density through territorial behaviour becomes less effective when food-quality declines and breeding intensity drops. But the mice on all grids stayed in breeding condition, so it is likely the the spacing behaviour mechanism was still operating efficiently. Redhead's hypothesis could be more successfully tested in a dry autumn, in which intensive breeding would not be expected to be maintained on control grids.

Table 5.1. Data for numbers of mice caught at usual trap-sites and at half-way trap-sites. Usual trap-sites were next to feeders.

Trap position	Usual trap-site		Half-way trap-site	
Grid number	4	7	4	7
Total mice	9	14	12	18
Recaptures	7	6	8	9
Adult females	4	5	5	6
Breeding females	4	4	4	5

Table 5.2. Sources of variation and degrees of freedom used in 2-way analysis of variance tests for treatment effects on numbers of mice caught.

Source	Degrees of freedom
Farm	1
Food	1
Cull	1
Food x cull	1
Residual	11
Total	15

Table 5.3. Sources of variation and degrees of freedom used in analysis of variance tests for treatment effects on Instantaneous Rates of Decline.

Source	Degrees of freedom
Farm	1
Food	1
Cull	1
Period	3
Food x cull	1
Period x food	3
Period x cull	3
Period x food x cull	3
Residual	47
Total	63

Table5.4. Food types and protein concentrations in the diet of mice on high and low quality foodgrids.

Food type	Protein concentration % dry weight	High - quality food grids (n = 46 stomachs)			Low - quality food grids (n = 20 stomachs)		
		Mean % volume	Estimated % dry weight	Estimated % protein*	Mean % volume	Estimated % dry weight	Estimated % protein*
Rice	8.0	42.3	46.6	3.73	93.7	96.7	7.74
Oats	10.8	26.6	27.1	2.93	-	-	-
Sunflower	18.8	26.0	24.6	4.62	-	-	-
Other dicot seed	19.0	0.9	0.8	0.15	2.8	2.5	0.48
Invertebrate	50.6	0.3	0.1	0.05	0.5	0.2	0.10
Other plant tissue	4.0	3.9	0.8	0.03	3.0	0.6	0.02
	TOTAL	100.0%	100.0%	11.5%	100.0%	100.0%	8.3%

* See Section 5.2.6.

Table 5.5a. Numbers of mice caught (n)

Food	High-quality food								Low-quality food							
Culling	Culled				Unculled				Culled				Unculled			
Farm	One		Two		One		Two		One		Two		One		Two	
Grid number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Trap session																
T1	30	20	34	34	28	38	31	25	40	25	27	25	45	30	27	22
T2	60	44	53	22	57	53	25	36	50	45	20	19	37	47	13	20
T3	51	54	32	36	47	65	30	33	36	74	25	13	62	49	13	25
T4	36	40	36	32	43	38	23	32	16	21	20	20	30	33	17	29
T5	44	44	50	48	60	46	33	41	22	55	17	33	38	41	23	30

Table 5.5b. Variance ratios from analysis of variance tests for treatment effects on the number of mice caught

Trap session	Treatment			
	Farm $F_{(1,14)}$	Food $F_{(1,13)}$	Culling $F_{(1,12)}$	Food x culling $F_{(1,11)}$
T1	1.35	0.00	0.17	0.01
T2	30.41**	8.71*	0.56	0.07
T3	31.74**	1.55	0.01	0.00
T4	5.79*	22.21**	1.45	4.02
T5	4.07	8.29*	0.00	0.09

* $p<0.05$
** $p<0.01$

For method see Appendix 2f.

Table 5.6a. Numbers of adult females caught (f)

Food	High-quality food								Low-quality food							
Culling	Culled				Unculled				Culled				Unculled			
Farm	One		Two		One		Two		One		Two		One		Two	
Grid number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Trap session																
T1	6	4	5	4	2	12	1	3	11	3	2	4	11	6	1	5
T2	8	9	7	4	12	8	3	11	9	5	5	3	8	12	1	3
T3	17	10	14	5	12	22	12	8	8	10	3	3	13	10	6	8
T4	10	13	11	10	10	15	4	3	4	5	3	5	5	6	4	7
T5	12	14	12	15	19	19	9	11	7	25	5	13	10	13	4	7

Table 5.6b. Variance ratios from analysis of variance tests for treatment effects on the numbers of adult females (f)

	Treatment			
Trap session	Farm $F_{(1,14)}$	Food $F_{(1,13)}$	Culling $F_{(1,12)}$	Food x culling $F_{(1,11)}$
T1	6.16*	0.25	0.03	0.11
T2	10.58**	2.34	0.59	0.15
T3	9.99**	8.22*	2.38	0.14
T4	3.78	11.74**	0.42	2.48
T5	5.05*	1.99	0.33	0.11

* $p<0.05$
** $p<0.01$
For method see Appendix 2f.

Table 5.6c. Differences in deviance (1 d.f.) from logistic regression analysis tests for treatment effects on the proportion of adult females in the mice caught (f/n)

	Treatment			
Trap session	Farm	Food	Fulling	Food x culling
T1	9.533**	0.176	0.055	0.278
T2	0.007	0.049	1.772	0.002
T3	2.011	5.052*	3.523	0.718
T4	0.982	1.864	1.768	0.274
T5	2.922	0.202	1.092	4.786*

* $p<0.05$
** $p<0.01$
For method see Appendix 2g.

Table 5.7a. Numbers of recaptures (m) and total numbers of mice (n)

Food		High-quality food								Low-quality food							
Culling		Culled				Unculled				Culled				Unculled			
Farm		One		Two		One		Two		One		Two		One		Two	
Grid		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Trap session																	
T2	m	12	5	9	6	8	12	3	7	3	5	3	2	6	7	3	0
	n	60	44	53	22	57	53	~~25~~	36	50	45	20	19	37	47	13	20
T3	m	13	6	9	10	15	15	5	10	7	5	5	2	10	13	4	5
	n	51	54	32	36	47	65	30	33	36	74	25	13	62	49	13	25
T4	m	9	13	15	8	12	15	7	8	5	5	6	5	12	4	7	12
	n	36	40	36	32	43	38	23	32	16	21	20	20	30	33	17	29
T5	m	12	12	10	19	24	19	13	16	6	23	5	12	21	14	5	10
	n	44	44	50	48	60	46	33	41	22	55	17	33	38	41	23	30

Table 5.7b. Differences in deviance (1 d.f.) from logistic regression analysis tests for treatment effects on the proportion of recaptures in the mice caught (m/n)

	Treatment			
Trap session	Farm	Food	Culling	Food x culling
T2	0.129	4.263*	0.258	0.712
T3	2.076	3.713	3.672	1.004
T4	0.608	0.080	0.206	0.373
T5	1.494	0.416	3.510	1.542

* $p<0.05$

For method see Appendix 2g.

Table 5.8a. Numbers of recaptured adult females (h) and total numbers of adult females (f)

Food		High-quality food								Low-quality food							
Culling		Culled				Unculled				Culled				Unculled			
Farm		One		Two		One		Two		One		Two		One		Two	
Grid number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Trap session																	
T2	h	4	3	1	0	2	2	0	1	2	0	1	0	1	2	0	0
	f	8	9	7	4	12	8	3	11	9	5	5	3	8	12	1	3
T3	h	6	3	4	1	3	4	2	3	2	1	0	1	1	4	1	3
	f	17	10	14	5	12	22	12	8	8	10	3	3	13	10	6	8
T4	h	4	7	8	1	4	8	2	3	3	1	2	1	3	2	2	4
	f	10	13	11	10	10	15	4	3	4	5	3	5	5	6	4	7
T5	h	6	6	6	9	11	12	7	7	2	13	3	5	8	7	2	4
	f	12	14	12	15	19	19	9	11	7	25	5	13	10	13	4	7

Table 5.8b. Differences in deviance (1 d.f.) from logistic regression analysis tests for treatment effects on the proportion of adult females that were recaptures (h/f)

	Treatment			
Trap - session	Farm	Food	Culling	Food x culling
T2	3.880*	1.936	1.930	0.259
T3	0.073	0.406	0.121	1.237
T4	0.039	0.177	0.822	0.000
T5	0.072	0.213	4.019*	0.025

* $p<0.05$

For method see Appendix 2g.

Table 5.9a. Numbers of breeding females (r) and numbers of adult females (f)

Food		High-quality food								Low-quality food							
Culling		Culled				Unculled				Culled				Unculled			
Farm		One		Two		One		Two		One		Two		One		Two	
Grid number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
trap session																	
T1	r	4	2	4	4	1	8	1	2	4	1	2	4	8	6	0	4
	f	6	4	5	4	2	12	1	3	11	3	2	4	11	6	1	5
T2	r	6	5	1	2	5	2	1	3	2	3	3	0	2	9	0	1
	f	8	9	7	4	12	8	3	11	9	5	5	3	8	12	1	3
T3	r	13	8	9	4	7	10	11	7	5	4	1	2	3	5	3	2
	f	17	10	14	5	12	22	12	8	8	10	3	3	13	10	6	8
T4	r	6	6	7	9	7	8	4	2	1	2	2	2	0	1	1	4
	f	10	13	11	10	10	15	4	3	4	5	3	5	5	6	4	7
T5	r	5	6	10	13	15	9	6	7	3	8	1	7	3	5	3	2
	f	12	14	12	15	19	19	9	11	7	25	5	13	10	13	4	7

Table 5.9b. Differences in deviance (1 d.f.) from logistic regression analysis tests for treatment effects on the proportion of breeding females in the adult females caught (r/f)

	Treatment			
Trap session	Farm	Food	Culling	Food x culling
T1	4.246*	0.018	1.497	1.520
T2	3.372	0.002	0.359	2.114
T3	2.308	11.262**	2.371	0.153
T4	4.697*	12.522**	0.002	1.593
T5	6.858*	11.537**	0.006	0.013

* $p<0.05$
** $p<0.01$

For method see Appendix 2g.

Table 5.10. Variance ratios from tests for treatment effects on the slopes in the regression lines of $\log_e$ weight on $\log_e$ length for males

Trap session	Variance ratio	Degrees of freedom
T1	0.576	7, 369
T2	1.933	7, 352
T3	1.817	7, 323
T4	3.722*	7, 231
T5	0.987	7, 288

* $p<0.05$
For method see Section 3.2.4.

Table 5.11. Variance ratios from analysis of covariance tests for treatment effects with log Length as the co-variate, and log weight as the variate.

Trap session	Farm	Food	Cull	Food x cull	Degrees of freedom
T1	30.399***	3.560	2.909	4.337*	1, 379
T2	1.021	0.146	1.[illegible]	5.915*	1, 362
T3	6.7[illegible]**	1.[illegible]	1.[illegible]	0.926	1, 333
T4	2.449	[illegible].182	1.553	1.966	1, 241
T5	30.273***	0.188	0.037	0.495	1, 299

* $p<0.05$
** $p<0.01$
*** $p<0.001$
For method see Appendix 2h.

Table 5.12. Body fat contents. Mean values ± one standard error, for % body fats for mice caught on high-quality and low-quality food grids. Sample sizes are given in brackets.

Sex	Treatment			
	High-quality food		Low-quality food	
Female	19.3+0.6	(22)	21.1+0.7	(10)
Male	17.2+0.5	(15)	17.9+0.7	(15)
Combined	18.5+0.5	(37)	19.2+0.6	(25)

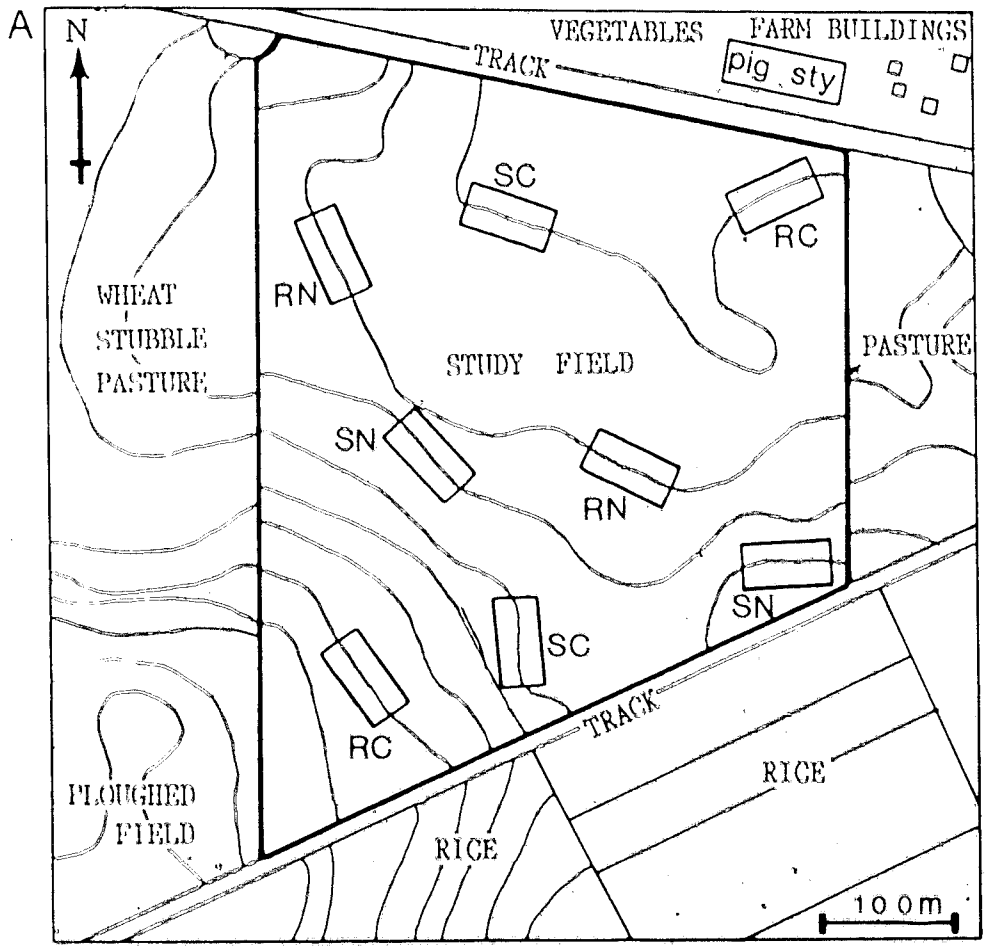


Figure 5.1. The two rice farms used as study sites in the second field experiment, showing the locations of experimental treatment grids. A) Farm 1. and B) Farm 2. Two factors, each set at two levels in a 2^2 factorial design constituted the experimental treatments applied on grids:

Factor 1 = food quality:
- S = high quality (protein supplemented diet)
- R = low quality (natural rice diet).

Factor 2 = population density:
- N = high density (natural population density)
- C = low density (juveniles culled from population).

This gave four treatment combinations: SN, SC, RN and RC.

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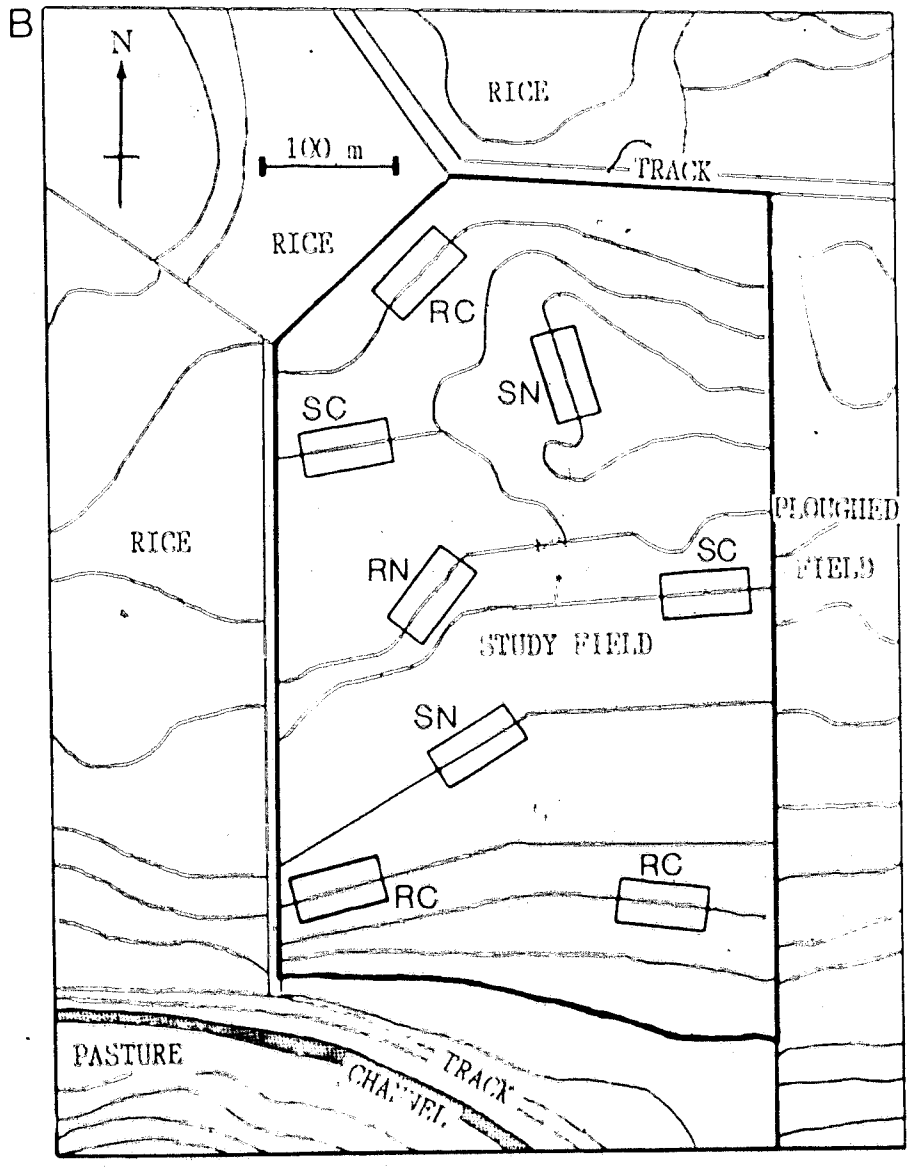


Figure 5.1 Cont. B.

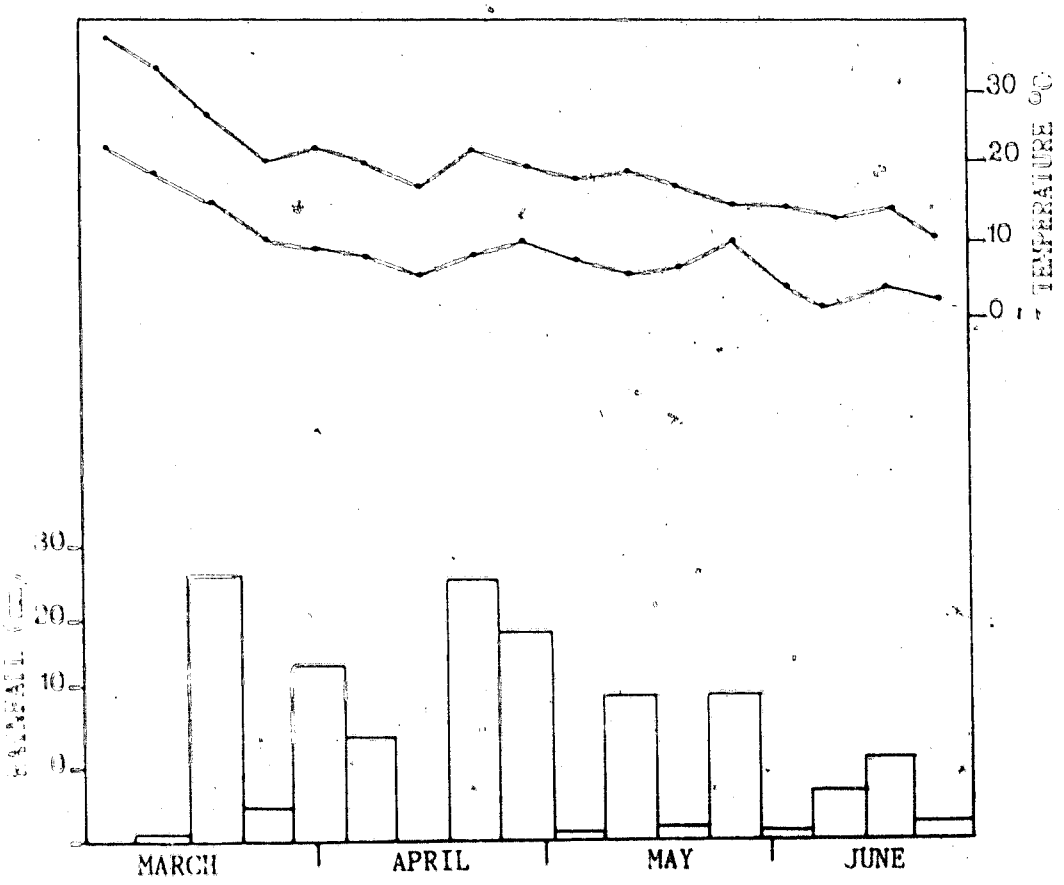


Figure 5.2. Temperature and rainfall data for Griffith NSW over the experimental period March to June 1983. Mean maximum and minimum weekly temperatures are given, and total weekly rainfalls.



Figure 5.3. Contour banks had a moderate weed cover. Species shown include saffron thistle in centre, and blackberry nightshade at right. A sheep fence erected around the study grid is visible in the middle distance.



Figure 5.4. Beer cans were used as feeders. The oats and sunflower seeds that were scattered around the feeders germinated, and these sprouted seeds were often eaten by mice.

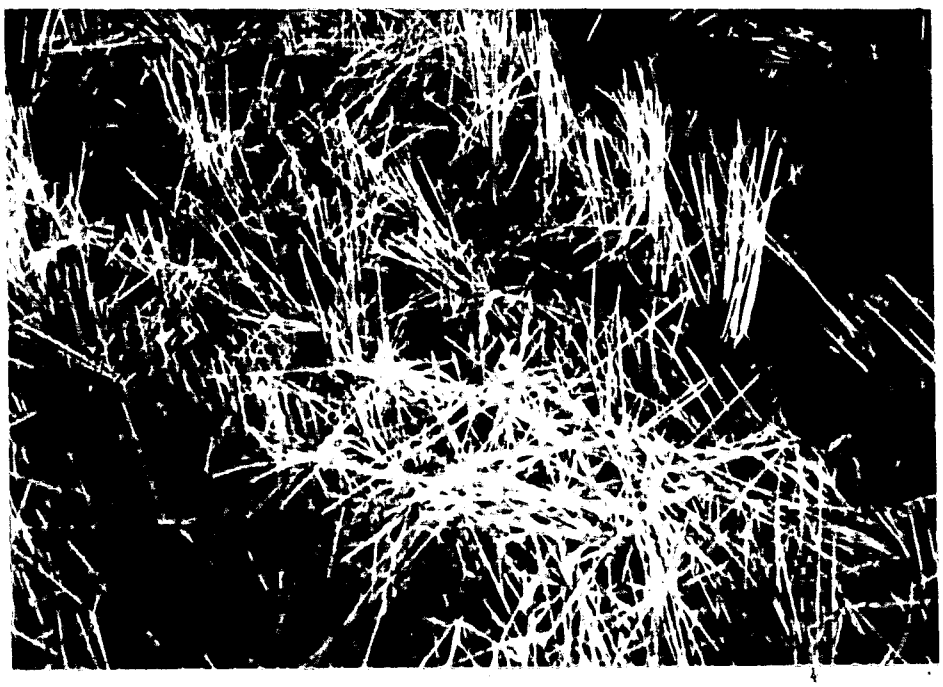


Figure 5.5. The ground in the study fields remained wet throughout the duration of the second field experiment. After harvest there was still plenty of rice grain left amongst the rice straw

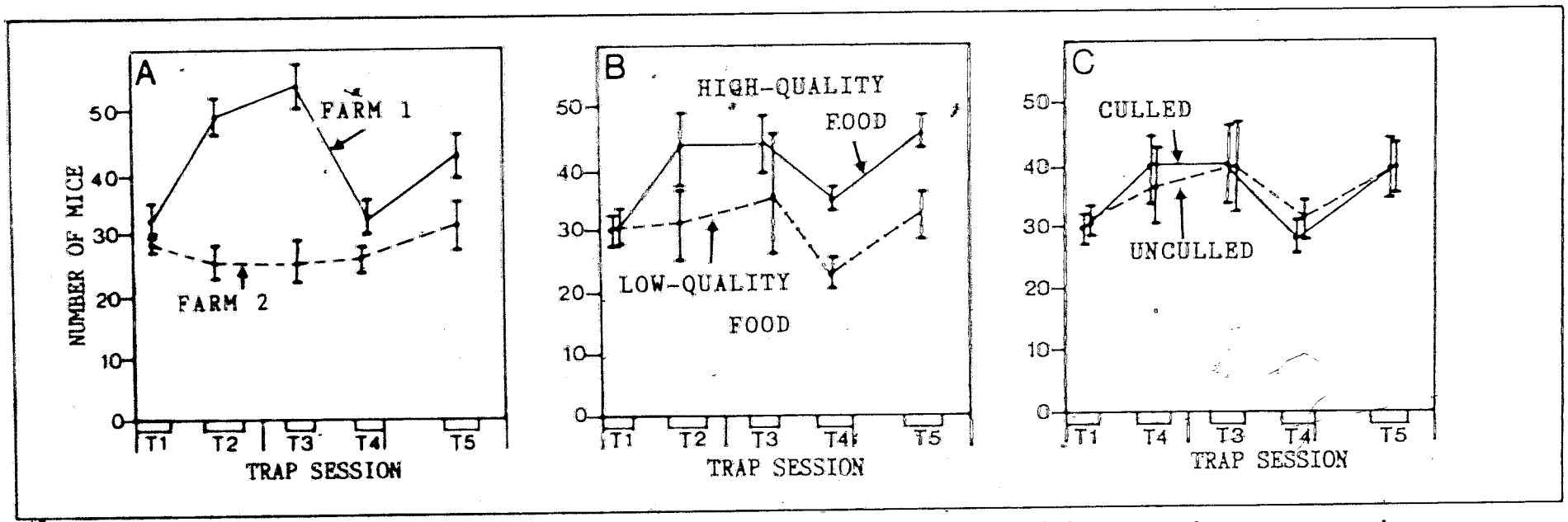


Figure 5.6. Treatment means for total numbers of mice caught (n) in each trap-session. A) Farms, B) Food quality, and C) Culling. The statistical analyses of these results are presented in Table 5.5b.

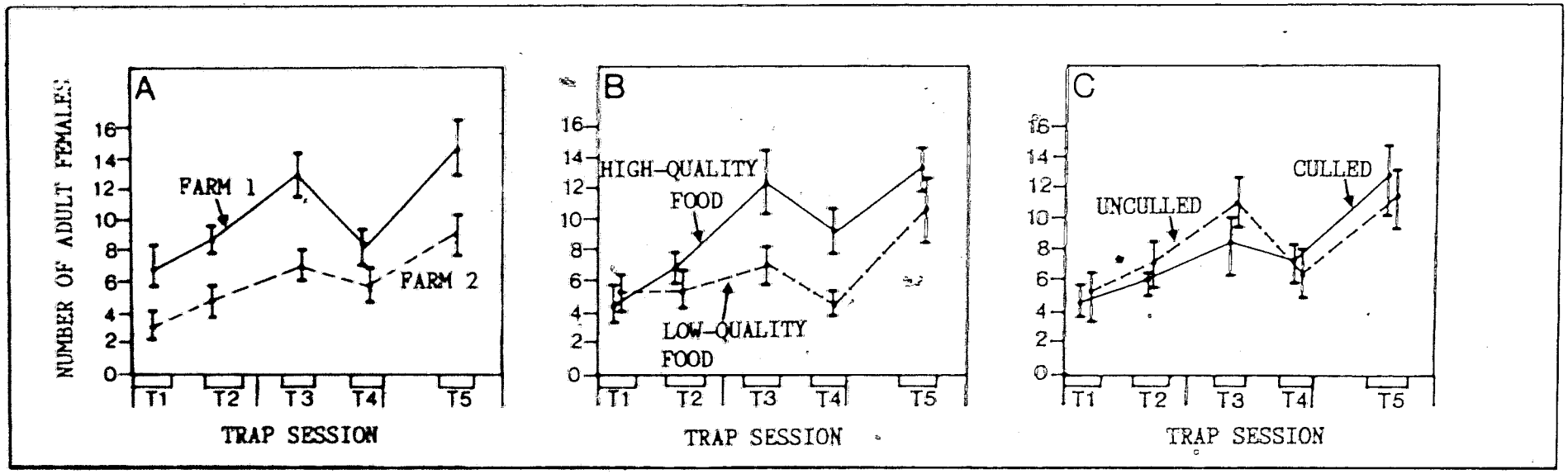


Figure 5.7. Treatment means for adult female numbers caught (f) in each trap-session. A) Farms, B) Food quality, and C) Culling. The statistical analyses of these results are presented in Table 5.6b.

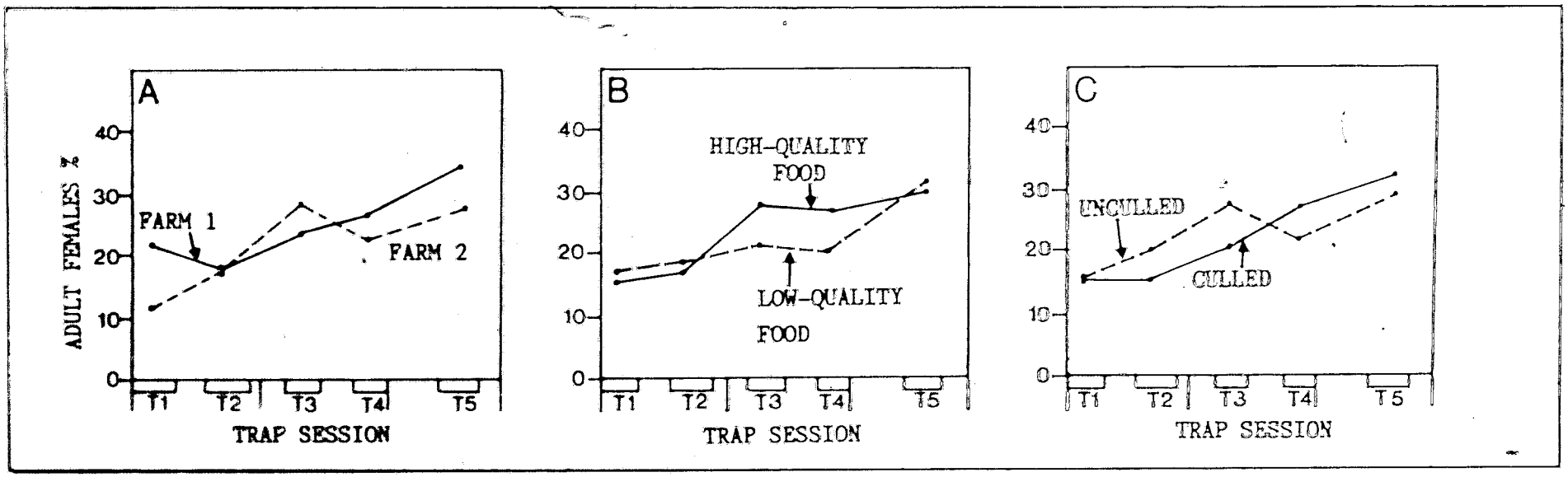


Figure 5.8. Fitted treatment means for the proportion of adult females in the mice caught (f/n). A) Farms, B) Food quality, and C) Culling. The statistical analyses of these results are presented in Table 5.6c

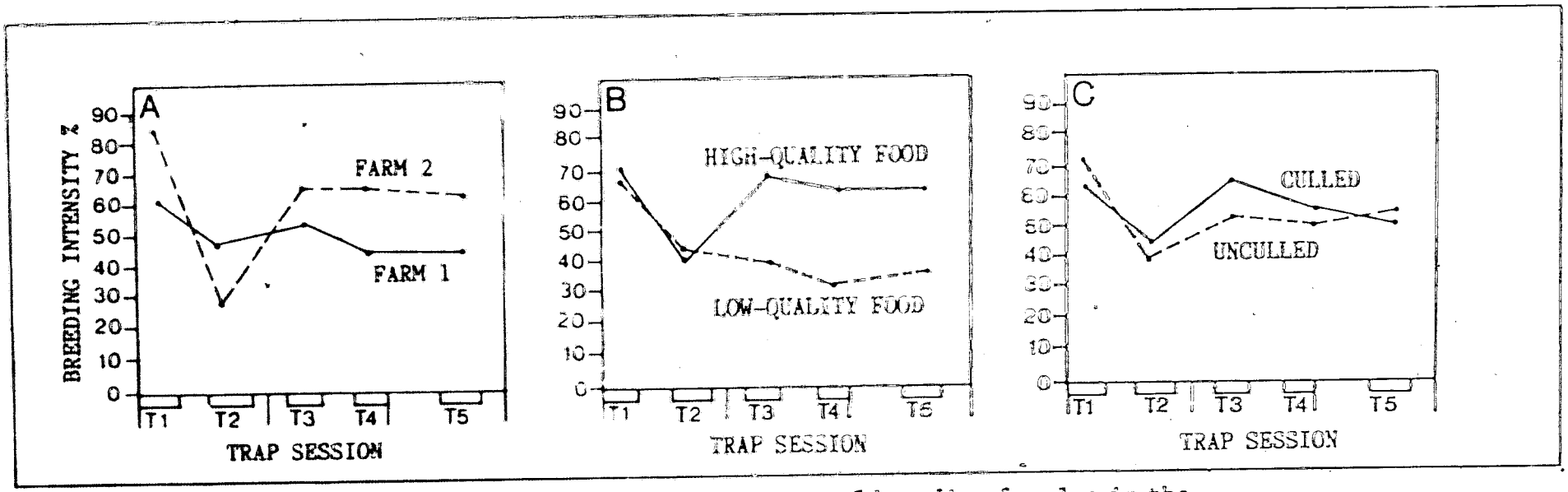


Figure 5.9. Fitted treatment means for the proportion of breeding females in the adult females caught (r/f). A) Farms, B) Food quality, and C) Culling. The statistical analyses of these results are presented in Table 5.9b.

CHAPTER SIX

DISCUSSION AND CONCLUSIONS

The main purpose of this chapter is to integrate the results from the different sections of the study. These results are then discussed in relation to conclusions drawn from previous studies on the effects of food limitation of breeding on house mice and other species. Consideration is then given to the results of this study in the context of mouse-plague control and of future research directions.

6.1. RELEVANCE OF THE STUDY

Plagues or outbreaks occur across the animal kingdom and there is no general explanation for their occurrence (Kikkawa 1977). Outbreaks of house mice have been attributed to a massive increase in breeding habitat because of soil moisture changes (Newsome 1969a), to the effects of drought (Saunders and Giles 1977), to increased winter survival (Berry 1981a) and, more often, to increased breeding in response to unusually abundant or high-quality food supplies (Finlayson 1939; Newsome 1970; Naumov 1972; Bronson 1979; Pryor and Bronson 1981; Redhead 1982). The food supply model of mouse plague formation can be split into two hypotheses: 1) that the breeding of house mice is usually limited by one or more aspects of food supplies; and 2) that increased breeding will cause an increase in population density. The study of house mice in the MIR by Redhead (1982) indicated a need for a detailed investigation of the first of these two hypotheses. The present study consequently investigates the role of food supply in limiting the reproduction of house mice in the MIR. In the main, other factors, such as changes in survival and changes in

habitat quality, are not investigated, as the study was not intended to encompass the whole field of mouse demography and plague formation.

6.2. DESCRIPTION AND EXPERIMENTATION: AN INTEGRATION OF THE MAIN RESULTS

The questions addressed were directed at developing a better understanding of how food quality and supply might determine the breeding performance of house mice on irrigated cereal farms. The research involved a combination of descriptive work, laboratory experiments and field experiments, as each of these approaches had advantages that made them suitable for particular areas of the study.

The first part of the study, which described food supplies, diet and breeding performance, was conducted to generate hypotheses regarding the relationship between these factors. The results showed that 1) the mice were mainly granivorous, as had been found previously for mice in cultivated habitats (Naumov 1940; Sakhno 1957; Kami 1966; Whitaker 1966; Houtcooper 1987; Smiet *et al.* 1980; Fulk *et al.* 1981), 2) the types of seeds and supplementary foods the mice ate differed between season and habitats, which had also been previously reported (Naumov 1940; Sakhno 1957; Whitaker 1966; Houtcooper 1987; Smiet *et al.* 1980; Fulk *et al.* 1981), and 3) the mice had a seasonal pattern of breeding, in common with other studies (Naumov 1940; Breakey 1963; Pearson 1963; Lidicker 1966; Batten and Berry 1967; Berry 1968; Newsome 1969a,b; Thomson 1979; Myers 1974; Morton 1978; Stickel 1979; Smiet *et al.* 1980; Williams and Wilson 1980; Chapman 1981; Gleeson 1981; Pelikan 1981). The timing of both the onset and cessation of breeding in the different habitats appeared to be closely linked to changes in food supply and diet.

These apparent links led to the formulation of two hypotheses, as follows.

First, the most obvious link between food supplies and breeding was the time fresh grass and grain seeds became available and the time breeding started. The experiment described in Chapter Three tested the hypothesis that breeding of mice in rice fields in spring is limited by the food supplies which are inadequate in 1) energy or 2) quality (Hypothesis 1). The experiment was designed to test whether breeding was limited by inadequte amounts of either energy, nutrients, or GA_3 in the food supply. The results of this experiment showed conclusively that breeding in spring was limited by food supplies. Because of a high level of within-treatment variance, however, the experiment was not powerful enough to discern whether it was the energy content or the nutrient quality of the natural food that was inadequate. But as even the poorest quality supplementary food, plain wheat grain, improved breeding performance, it is suggested that energy was limiting.

Second, the results of the descriptive study indicated that food supplies appeared to be limiting for breeding in rice stubble fields in early autumn. Breeding intensity declined in this habitat while grain supplies were still plentiful, suggesting that there was an adequate supply of energy, but as the mice were eating a diet of nearly pure rice grain at this time, it seemed likely that the diet would be inadequate in nutritional quality to support breeding. This led to the hypothesis that breeding in autumn rice fields is limited by poor food quality (Hypothesis 2). Several factors may act in concert to limit breeding in the field (Section 1.1), and Redhead (1982) hypothesized that poor-quality food caused an initial suppression of breeding, which was reinforced by social suppression associated with increasing population density. Therefore the effect of population density on

breeding was tested in addition to the effects of food quality in the field experiment conducted to test Hypothesis 2.

To obviate the problem of high within-treatment variance caused by uncontrolled environmental variables found in the first field experiment, two approaches to testing Hypothesis 2 were taken: 1) Sources of variance were controlled by experiments testing the hypothesis for caged mice kept under laboratory conditions. This allowed temperature, light, food availability, social factors, genotype, body weight and age of mice to be controlled (Chapter Four). 2) In the field experiment conducted to test the hypothesis, the number of treatments was restricted to only four, so that within-treatment replication could be maximised, giving the experiment the maximum power to discern treatment effects (Chapter 5). The relative merits and disadvantages of laboratory experiments versus field experiments have been discussed earlier (Sections 3.1 and 4.1).

The results of the laboratory experiments which were conducted to determine which food supplements have a significant effect on the breeding performance of mice, showed that supplements of milk-ripe seeds or mealworms did not improve breeding performance, but that small supplements of sprouted rice grain did. Because many changes in chemical composition occur at germination (Section 4.3), it is unclear which nutrients or chemicals that were present in germinated grain but not in mature grain were responsible for the observed effect. Of the three pure supplements to rice grain diets, which were also tested, supplements of GA_3 and vitamin A did not affect breeding performance, but casein (protein) supplements improved both breeding intensity and mean litter size. Two high-protein seeds, oats and sunflower seeds, were then tested to see if they also supported a better breeding performance than rice grain. The result was positive, [redacted] these seeds were selected as a supplementary high-

quality food to use in the subsequent field experiment to test Hypothesis 2. The results of that experiment (Chapter 5) showed that the breeding of mice in rice stubble fields in autumn was limited by the food quality. The limiting nutrient was probably protein, but other nutrients present in the supplementary seeds may have contributed to the improved breeding performance. The experiment failed to test the effect of population density on breeding performance, because the culling treatment, which was conducted to reduce numbers, failed to do so.

Although Bronson (1979) considered it would be difficult to separate and examine individually the various environmental factors which could act to limit the breeding of house mice in the field (Section 2.1), the series of experiments summarized above show clearly that breeding was limited by food supplies at both ends of the breeding season. The supply of energy was probably the main factor in spring, and the quality of the food, particularly its protein content, was probably the main factor in autumn.

6.3. FACTORS LIMITING BREEDING IN HOUSE MOUSE POPULATIONS

In many studies of natural house mouse populations, a fairly large proportion of females have been found not to breed (Laurie 1946; Smith 1954; and Breakey 1953). Citing these studies as examples, Pryor and Bronson (1981) interpreted the low levels of fertility as being attributable to diet quality, and suggested that the mice were living in habitats 'not nutritionally capable of supporting more than an intermediate level of breeding even at the most suitable times of year'. Pryor and Bronson thought it was not simply an energy shortage, but they did not suggest which nutrients were most likely to be inadequate.

Correlations between timing of breeding and available food supplies for natural populations of house mice, have previously been suggested by Newsome (1969a) in wheat fields in South Australia, by Newsome and Corbett (1975) in semi-arid inland Australia, by King (1982) in beech forests in New Zealand, and by Redhead (1982) in rice fields in the MIR. Demonstrations of a causal relationship between food supply and breeding of house mice by supplementary feeding experiments, have previously been shown by DeLong (1967) in oldfields in California and by Newsome (1970) in reedbeds in South Australia, but Redhead (1982), did not get a breeding response to supplementary food in rice fields in the MIR in winter. The present study, however, is the first to demonstrate that food nutrient quality can limit the breeding of a natural house mouse population.

Even when food supplies are adequate, other factors act to limit breeding in the field. When mice in the laboratory have their breeding performance impaired by diets deficient in energy or nutrients, they usually demonstrate the ability to recover full fertility when their diet is made adequate, and exceptions occur only when vitamin or mineral deficiencies are so severe or prolonged that permanent damage to organs occur (Cerecedo and Vinson 1944; Ball *et al.* 1947; Carr *et al.* 1949; McCarthy and Cerecedo 1952; Visscher *et al.* 1952; McClure 1966; Truscott *et al.* 1974; Zamiri 1978). As such extreme deficiencies probably rarely occur in field populations eating natural diets, house mice which are food limited in the field should have the ability to fully recover their fertility when food supplies are made adequate by supplementary feeding, and breeding should continue as long as food supplementation continues, unless factors in addition to food are responsible for the suppression of breeding. In the supplementary feeding studies of house mice conducted by DeLong (1967) and Newsome (1970), extra food increased the proportion of females breeding, and breeding was prolonged through

winter, demonstrating that food supply was the limiting factor for breeding in this season. But in neither study were all adult females found to breed on feeding plots through winter, and in DeLong's study, breeding ceased altogether on his feeding plots in the second summer, after about ten months of supplementary feeding. He suggested that social suppression was responsible, as high population densities were reached on his feeding plots. In the study conducted by Redhead (1982), supplementary feeding of non-breeding house mice in a rice stubble field in winter caused no breeding response. He considered this as evidence that the autumn cessation of breeding of mice in this habitat was not due to a calorie shortage. But the provision of extra food attracted mice onto his feeding plots, so that after a month of supplementary feeding density indexes on feeding plots were ten times those on the control plots. It would seem likely that this increased density would have caused social inhibition of breeding on his feeding plots even if all other conditions were suitable. Therefore it is unclear from the results of this experiment whether breeding was food limited prior to the start of his supplementary feeding. In both field experiments the present study, supplementary food improved breeding performance, but breeding intensity never rose above 70% in either experiment on supplementary on supplementary feeding sites (Figures 3.5 and 5.9). Also, few females were found to be simultaneously pregnant and lactating in either experiment, indicating that conceptions at the post-partum oestrus were rare.

Hence, four experiments, including two in the present study, with supplementary feeding of house mice, have demonstrated that food limits breeding, but all have also indicated that there are clearly additional factors involved, and a fifth supplementary feeding experiment conducted by Redhead, showed some factor other than food limitation completely prevented breeding. Further evidence that such additional factors operate in winter comes

from the comparison of laboratory studies conducted on caged mice fed nutrient-deficient diets, which usually continue some breeding, albeit restricted, (Table 4.1 and Section 4.3), with field studies of mice, which usually show a complete cessation of breeding in winter (Figure 2.6 and Section 3.1).

Several possible factors acted in addition to food supply to inhibit breeding in the present study. These included i) temperature, ii) social suppression, and iii) sterility, and these factors are discussed briefly below.

i) The evidence for the suppression of breeding of house mice by low temperatures has been reviewed earlier (Section 1.1). Low temperatures, especially combined with wet or variable conditions, may add to the effects of inadequate food supplies to further depress breeding. In the last month of the autumn experiment of the present study, minimum temperatures were falling around 3°C, (Figures 5.2 and 5.9b) and this may have supressed breeding, as an ambient temperature of 3°C was found by Pryor and Bronson (1981) to suppress breeding in caged wild-strain mice. While it is known that mice can genetically, physiologically and behaviourally adapt to breeding at low temperatures, many of these adaptations are not immediate, and when reproductively active house mice are initially exposed to a decline in temperature, as at the onset of winter, an initial decline in breeding can be expected, before a slow recovery occurs if low temperatures persist.

ii) Social suppression may also operate to inhibit breeding in field populations of house mice. Berry (1981a,b) has pointed out that house mice are adaptable in their reproductive ecology. In the MIR, the period of nutrient restriction is very unlikely to be more than a few months in duration, as an annual supply of fresh seeds becomes available soon after the onset of each irri-

gation season. It could be advantageous for house mice under these conditions to have social adaptations to maximize survival rather than reproduction through this period. Average litter sizes are small at the end of the irrigation season (Section 2.3.3), and the young in these litters would probably be underweight, given the poor quality of the food (Zamiri 1978; Widdowson 1981). It may be a better option for a female, in terms of biological fitness, to cease breeding in autumn, rather than to use her body reserves to produce a small, underweight litter which may not survive the winter. In producing a litter she would probably greatly reduce her body reserves and hence her own chances of surviving the winter. The alternative, to store body fat and nutrients, and optimize her survival chances through to the spring, may be more viable, as in spring the diet quality is high, and females usually show high fertility and fecundity at this time (Section 2.3.3). Hence the advantages to evolving a mechanism to switch off breeding when food resources become poor, but before they are directly limiting, may be considerable for mice in this area. Such self-regulation would not be an alternative to regulation by food, but rather be an addition to it that comes into play at a time before food supplies become directly limiting, with available food supplies and their quality determining when self-regulation is implemented, and hence the point at which breeding is suppressed in relation to food supplies.

Mechanisms do exist for such self-regulation of breeding in house mice populations, and these have been studied mainly for enclosed or caged mice as reviewed earlier (Section 1.1). Redhead (1982) considered that at least some of these mechanisms operate in mouse populations on MIR rice farms. Hansson (1979) pointed out that 'Many possible nutritional effects . . . on reproductive output, have been suggested by the self regulation schools to be caused by genetic changes or social stress'. This makes it difficult, in studies of field populations to separate

direct effects of inadequate food supplies on breeding, from earlier executed self-regulation effects, related to food supply, such as those indirectly imposed by genetic changes (Chitty 1967), physiological changes due to crowding (Christian 1971), or behavioural conventions (Wynne-Edwards 1962). Redhead (1982) reported no evidence for either Chitty-type or Christian-type regulation of breeding for mice in the MIR, but his data on dispersal patterns and sex ratios led him to suggest that social suppression, perhaps via pheromonal cueing, was likely.

iii) A further possible cause of the failure of some mice to breed is sterility. Many of the mice caught in the MIR in the present study were kept as breeding pairs on ballanced pellet diets, yet never produced litters. Wallace (1981) found about half the wild-stock females she tested in the laboratory were infertile, and she suggested this could have been associated with a previous favus infection. Redhead (1982) suggested infection by *Actinobacillus moniliformis*, present in the populations monitored in the present study, could adversely affect breeding performance. The resistance of mice to infection may in turn be affected by their nutritional status (Schneider 1956; Bounous and Kongshavn 1982). Some chemicals found in plants are also known to cause infertility in mice (Section 2.4), and these may have been present in the natural foods mice were eating.

6.4. FOOD LIMITATION OF BREEDING IN OTHER SPECIES

The limitation of breeding by the nutritional quality of the food, rather than by its quantity or energy content, has been little studied for rodents, and only for some microtine rodents has this subject been investigated in any detail. Hoffmann (1958) showed a direct correlation between litter size and the protein content of the food for field populations of *Microtus montanus*

and *Microtus californicus*, and suggested that this was a causal relationship. Batzli and Pitelka (1971) suggested that diet quality might determine the timing of breeding in field populations of Microtus californicus as they bred on a diet of grass stems and leaves, but not when they switched to a diet of grass seeds. Cole (1977) also found that the reproductive performance of field populations of *Microtus ochrogaster* was strongly correlated with the quality of their forage, and this led Cole and Batzli (1978), to predict that breeding performance would be affected by the availability of high-quality food. They demonstrated this with a supplementary feeding experiment, and showed that field populations fed a high-quality rabbit pellet diet had higher breeding intensity and a larger mean litter size than controls on a bluegrass diet (Table 1.1). Getz *et al.* (1979) compared the breeding performance of *Microtus ochrogaster* in habitats with different forage conditions and suggested that the length of the breeding season is also determined by food availability. Barkley *et al.* (1980) constructed a model of the nitrogen (protein), phosphorus and calcium requirements of *Lemmus sibiricus* for maintenance, growth and reproduction, and the amounts available in their food supply, and concluded that nutrient requirements may not always be adequate for reproduction even when energy requirements are met, and Batzli and Pitelka (1983) suggested that the reproductive performance of *Lemmus sibiricus* varies between habitats in response to differences in diet. The role of plant chemicals, such as 6-MBOA in stimulating the breeding of *Microtus montanus* has been reviewed earlier (Section 2.4).

The conclusions drawn from the present study, regarding limitation of breeding by poor food quality, are similar to those proposed by previous authors for microtine rodents. But some of those studies also relate to the nutrient recovery hypothesis, which states that cycles in numbers of small herbivores are a product of a feedback loop in which population density determines

grazing pressure, and hence food availability and quality, which in turn determines future population density (Lack 1954; Pitelka 1964; Schultz 1964; Batzli and Pitelka 1971; Hansson 1979). This theory is probably largely inapplicable to granivorous house mice, because as seed eaters their grazing pressure is unlikely to affect future food availability, and more importantly, on MIR farms, the factors which decide food availability are external weather patterns and farming practices.

The limitation of breeding by food availability, as opposed to food nutrient quality, has been the subject of more frequent investigation. Many rodent species restrict their breeding to particular seasons. In late pregnancy and during lactation the mother and offspring are most susceptible to detrimental environmental influences (Sadlier 1969). Zucker *et al.* (1980) propose that an adequate food supply for parents and young is the most important ultimate factor underlying seasonal reproduction for many rodent species. Animals that reproduce seasonally have been rated along a facultative-obligative continuum (Negus and Berger 1977). Facultative breeders live in relatively unpredictable environments where anticipatory adjustments to optimal conditions are impossible. They must respond to favourable conditions once they occur. In the r - K continuum (MacArthur and Wilson 1967; French *et al.* 1975; Southwood 1977), the house mouse has often been considered a classic example of an animal at the extreme r end, and Berry (1981b) called house mice 'r-selected weeds', that need to 'be able to breed rapidly, tolerate a wide range of conditions, and adjust quickly to changes in its environment'. The results of the present study fit this concept, to the extent that mice were shown to be able to rapidly respond in their breeding intensity to favourable food conditions. But how closely population densities are tied to breeding intensity and duration is still unclear.

Supplementary feeding experiments have frequently demonstrated that the breeding of rodents in the field is limited by food availability. Table 1.1 shows that supplementary food has increased breeding intensity, in nine species and increased the duration of the breeding season in nine species. In only four studies was it clearly documented that neither of these reproductive parameters changed when supplementary food was provided, and the species involved were *Mus musculus*, *Clethrionomys glareolus*, *Microtus californicus* and *Mastomys natalensis*. For the first three species, however, other studies summarised in the table found supplementary food did improved both breeding parameters, and although Taylor and Green (1976) found supplements of wheat grain did not cause aseasonal breeding in a field population of the forth species, *Mastomys natalensis*, they found an aseasonal wheat crop did. Possibly a chemical stimulus was present in the growing stages of the wheat crop, but absent from the mature grain. Hence food limitation of breeding appears to be a fairly widespread phenomena in natural populations of rodents.

6.5. RESULTS IN THE CONTEXT OF POPULATION REGULATION AND PLAGUE FORMATION

Increased breeding was associated with an eventual increase in density in eight of the species listed in Table 1.1, but the extent to which this is a causal relationship was unclear, as for seven species in other studies listed in the table, there was no improvement in breeding intensity or duration of breeding, yet there was still an increase in density associated with supplementary food. Hence the change in numbers recorded in the second group of studies must have been solely due to changes in survival or dispersal. Several of the authors suggested that population densities were being regulated by behavioural mechanisms (Fordham 1971, *Peromyscus maniculatus*; Cole and Batzli 1978, *Microtus*

ochrogaster; Taitt 1981, *P. maniculatus*; Taitt and Krebs 1983, *M. townsendii*). Thus although the results from the studies in Table 1.1 indicate that supplementary food can increase litter sizes as well as breeding intensity, it is still unclear what effect such increased breeding has on numbers, and different authors still have opposing opinions. For example, Cole and Batzli (1978) consider 'it seems clear that the quality of food supply strongly influences the density and demography of microtine rodents', while Tamarin (1983) considers 'there is strong evidence that neither the quantity nor quality of food limits voles'.

While the present study was restricted to investigating the effects of food quality and supply on breeding performance, the results are clearly applicable to the subject of population regulation. The theory that plagues are caused by increased breeding in response to increased food availability is frequently suggested (Finlayson 1939; Newsome 1970; Naumov 1972; Bronson 1979; Pryor and Bronson 1981; Redhead 1982). This study has shown food limitation of breeding at either end of the breeding season. Whether this means that improved food supplies will lead to a plague depends on whether population regulatory factors counterbalance the increased reproductive productivity. Kikkawa (1977) outlined the two opposing theories in current population regulation theory.

1) The first theory is that populations are self-regulating through feedback mechanisms that are density dependent (Smith 1935; Chitty 1967; Krebs 1978; Caughley and Krebs 1983). Tamarin (1983) thinks 'A strong theoretical framework to support the model of population regulation through behavioral interactions now exists', and reviews the literature on this subject. He considers that this model may not just be applicable to mammal populations, but also to birds, fish and insects. Proponents of

this theory suggest that most small mammal populations may be intrinsically regulated, and have self-regulatory mechanisms that lower rate of increase by behavioural, physiological or genetic means in response to an increase in density (Chitty 1967; Christian 1971; Krebs *et al.* 1973; Wynne-Edwards 1962).

2) The second theory is that populations are extrinsically regulated, and that an equilibrium density, which is a mechanical consequence of the interaction between a population and its food supply, is reached by animal populations (Nicholson 1933; Lack 1954; Andrewartha and Birch 1954; White 1978). Andrewartha and Birch thought the main factor limiting numbers of animals in natural populations is the shortage of time in which the environment is suitable for the rate of increase to be positive.

Lidicker (1978) considers it is necessary to integrate both of these theories into a multi-factorial model to create the appropriate intellectual framework to analyse problems in density determination for small mammal populations.

Although Tamarin (1983) supports the first of these two theories, he also points out that animals that are r-selected may exist predominantly in an unregulated mode until environmental vagaries, such as weather, act to reduce their numbers. The house mouse, as a species at the extreme r-end of the r-K continuum (Berry 1981b; Newsome and Corbett 1975; Stickel 1979), could be expected to fit this pattern. But many self-regulatory feedback mechanisms are thought to regulate house mouse populations and have been demonstrated in enclosed and caged populations (Christian 1956; Crowcroft and Rowe 1957; Petrusewicz 1963; Christian and Davis 1964; Drickamer 1975 and 1981; Lloyd 1975; Lidicker 1976; Butler 1980; Van Zegeren 1980). Berry (1981a) thought 'Maximum numbers in a mouse population with excess food and a non-varying physical environment seem to be mainly deter-

mined by suppression of successful breeding in females', but he also considers that both emigration and mortality are major factors when considering recruitment. One method by which mice may regulate population density is through territorial behaviour, which leads to 'pre-saturation emigration' motivated by social pressures; mainly of mice that are young or subordate, and there is evidence for this both from studies of enclosed mouse populations (Lidicker 1976; Butler 1980) and field populations (Anderson 1961 and 1978; Fitzgerald *et al.* 1981; Redhead 1982). Sage (1981), however, reviewed the evidence for social organization and population structure from cage, enclosure and field studies on house mice, and concluded that 'Most field studies report much less evidence of tightly organized populations' and Myers (1974) also found that 'feral house mouse populations are not divided into temporally stable, closed genetic units as are populations living in farm buildings'.

If house mouse populations are self-regulated, then the consequence of an increase in breeding due to increased food should be a compensatory increase in dispersal or mortality to counterbalance the increased reproductive input. Gilbert and Krebs (1981) pointed out that supplementary food does not usually cause numbers of small mammals to increase greatly, and made the generalization that provision of *ad libitum* food will usually only cause numbers to double, whereas much larger increases might be expected if populations did not act to self regulate density in the presence of unlimited food. But if house mice exist in an unregulated mode, the consequence of an increase in breeding due to an improvement in food supplies should be an increase in population density.

The generation of 'plague-like' numbers of house mice on supplementary feeding plots is often due, at least in part, to immigration by mice attracted to the extra food onto the

feeding plots, as found by DeLong (1967), Newsome (1970) and Redhead (1982). Newsome described the increase in numbers he recorded on his feeding plot as an 'experimentally produced mouse plague', but the implication that the increase was similar to that which occurs in natural outbreaks seems doubtful, as Redhead (1982) advanced evidence to show that an outbreak he monitored in the MIR in 1979-1980 was generated entirely by local breeding, and not by immigration of mice from other areas. Hence there is a need for further experiments to be conducted on mouse populations, which are designed to test whether population-regulatory processes act to counteract increases in population density that would otherwise result from food-induced increases in breeding. Until such information is available it will not be possible to fit the findings of the present study into a model linking food supplies to mouse plagues.

Berry (1981b) thinks that survival rates are an important factor in plague formation 'In every case where the causes of an explosive increase in numbers have been investigated, it has been found to result from a greater or more dense population of mice surviving an unfavourable period and able to reproduce at a high rate during a less stressed phase'. He gives as an example, the study by Pearson (1963) who found that mouse plagues in California follow mild winters. Redhead (1982 and 1983) considers both factors are important, and suggests that the number of mice surviving through the winter and their condition as it affects future litter size will determine outbreaks. He thinks in years when rainfall is high in autumn and early winter, large numbers of mice survive the winter, and their condition index ($\log_e$ weight adjusted for $\log_e$ length, Section 3.2.4) is higher than that of mice after dry winters. In the present study, the field experimental treatments were not continued for sufficient time to test this causal relationship, but in a laboratory test (Section 4.3.), there was no evidence that food quality affected

condition index, but food quality did affect litter size in caged mice, and breeding intensity in the field. Redhead describes unusually high rainfall as a 'plague trigger' that acts to extend the season when high-quality food is available, which in turn extends the breeding season, which leads eventually to the outbreak. Even if populations are directly limited by environmental factors, the sequence of events between the rainfall trigger and the mouse plague may be interrupted at several points, so that not all years of heavy rain will be followed by a plague.

The value of these conclusions for mouse plague control will only be evaluated by further experiments. Given the high reproductive potential of the house mouse, and their ability to realize this potential in the field when conditions are favourable, attempts at control aimed at reducing numbers by altering survival rates by poisoning or other mass killing exercises, may well be useless, as there will be rapid replacement of removed individuals. As this study has shown that breeding intensity is affected by food supplies, control measures directed towards lowering environmental quality through available food supplies may be more profitable and so better worth investigation. As the MIR is a food producing district, little could be accomplished towards reducing food supplies during the crop-growing season. However, Redhead hypothesized that the number of females surviving the non-irrigation season, and the size of their litters in spring, were important factors determining mouse numbers at the end of the irrigation season. Hence, any factors that affect female numbers or litter size in spring, may in turn affect the timing and magnitude of outbreaks. In the present study, the spring experiment (Chapter Four) showed that numbers of females in spring rice fields were significantly affected by available food supplies. The laboratory results described in Chapter Four, also show that litter sizes are affected by the food supplies though this was not been demonstrated in the field. Therefore

control methods directed at reducing food suppies in winter and spring by early burning, grazing or ploughing of stubble fields, and application of weedicide on any seeding grasses, are worth further investigation. Such measures, if successful, should cause little disruption of normal farming practices. This study also showed that spring crops of wheat and barley and the associated grasses that grow in these fields provide a rich food source for mice in spring. As the mice that breed up in these crops in spring probably migrate into rice fields in summer, it may be in the farmers' best interests not to grow these crops in years when conditions indicate that a mouse plague is likely, to prevent an early spring build-up of mice on their farms.

6.6. FUTURE DIRECTIONS

Rodent plagues are responsible for world-wide damage and loss to man's grain crops. For example, up to 20% of the rice grown in some Asian countries is lost to rodents (Hope *et al.* 1976). Thus there is an urgent need for greater understanding of the causes of rodent outbreaks, as this information is fundamental to more applied studies for improving prediction and control techniques. House mice are one of the most common rodents associated with man and his agricultural fields, and Redhead (pers. comm.) estimated that a plague of mice occurring across three Australian states in 1979-80 may have caused losses of around 40 to 50 million dollars.

There is still the need to determine why self-regulatory processes do not always act to counter the effects of increased breeding caused by improved food quality. Redhead (1982) considers that 'Improved nutrition associated with active plant growth during each irrigation season holds an ultimate sovereignty over the [population] regulatory forces so that, during the irrigation

season, breeding occurs regardless of which regulating force was effective previously'. He further suggests that 'reproductive stagnation regulated the population only during the dry seasons', and that 'high density alone was not enough to induce reproductive stagnation'. The results of the present study give support to the theory that improved food supplies will cause increased breeding in field populations. Further field experiments, of extended duration, are clearly needed to determine whether this will lead to plague formation. Experiments to determine the effect of food-induced increases in breeding on population numbers were beyond the scope of the present study. Although a breeding response to a change in food supply may show within three or four weeks, a delay of more than two months would occur before the additional mice born could mature to a trappable age so that an increase in population density in response to increased breeding could be monitored. Therefore the field experiments of the present study were of insufficient duration to test the second part of the hypothesis concerning the formation of plagues. Such experiments will need to closely follow survival and mortality rates, to see if these alter to compensate for increase reproductive productivity, in the density dependent manner described in Section 6.4.

A further direction is the need to follow up the effects of population density on the suppression of breeding. In the present study, the culling treatment conducted in the second field experiment failed to reduce numbers. A future experiment, conducted in a dryer season when recruitment is lower, might be more successful. Alternatively, increasing the intensity and frequency of culling might be effective.

Follow-up experiments are also needed to determine the generality of the conclusions of the present study. Hayne (1976) has emphasized the need for this type of replication over time

and location if the conclusions are to have generality. In particular, the new finding that food quality affects breeding performance in house mice will require substantiation by further field experiments. Rice grain is a particularly low-quality food, so the observation that poor food quality limits breeding intensity in rice fields may not apply to mice in fields where grain with a higher protein content is grown, such as wheat, oats and barley. The autumn in which the second experiment was conducted was unusually wet, which made it more favourable for breeding than an average season. Hence there is the need to replicate the experiment in an autumn with a normal rainfall, and further, to replicate the experiment in non-irrigated habitats.

As discussed above, (Section 6.4), regulation of breeding by food quality has been little studied in rodents. There is therefore the need to find out if the conclusions drawn from this study are applicable to other rodents. The study by Lam (1980 and 1983) suggests that *Rattus argentiventer* may be a likely candidate for limitation of breeding by food quality. He described the breeding seasons of *Rattus argentiventer* in rice fields in Malaysia, and found a clear link between time of crop ripening and breeding for this species. In fields where a single rice crop was grown in a year, there was only one breeding peak, whereas in fields where two crops were grown successively, there was a bi-modal peak in reproduction. In all cases, peak reproduction corresponded closely to the time of late flowering and early grain filling of the rice. Lam was uncertain whether the timing of breeding was a response to a chemical stimulus of the type described by Negus and Berger (1977), or a response to the nutrient or energy content of the food. The studies by Taylor and Green 1976 on *Mastomys natalensis*, and Redhead (1979) on *Rattus sordidus colletti*, suggest these species are also likely candidates for limitation of breeding by food quality.

"Another direction worth further investigation is the effect of food quality on other aspects of the breeding performance of caged mice. Long term experiments are needed to measure the mice's ability to produce successive litters, and the interval between litters. Deol and Truslove (1957) found both these factors are affected by diet quality. The role of sprouted grain in the improvement of breeding performance should also be further investigated. There is a need to identify the active component, to determine whether it is a chemical trigger, or simply a substance that meets a nutritional deficiency present in grain diets. Field experiments are also needed to determine whether inclusion of sprouted grain in the diet is a factor involved in the extension of the breeding season in wet autumns.

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APPENDIX ONE

Analysis of the commercial pellets fed to mice.

Fidelity feeds, Mecon 713, rat and mouse cubes. Registered under the stock feeds and Medicines Act, 1940 (NSW).

Ingredients listed by manufacturers:

Wheat; barley; oats; maize; wheaten pollard; wheaten bran; soya-bean meal; meat and bone meal; fish meal; vitamins A, D3, B1, B2, B6, B12, E; pantothenic acid; niacin; copper sulphate; ferrous sulphate; zinc oxide; magnesium oxide; potassium iodate; cobalt oxide.

Analysis provided by manufacturers:

Min. crude protein	22.00%
Min. crude fat	4.00%
Actual crude fat	4.50%
Max. crude fat	6.00%
Max. crude fibre	6.00%
Actual salt	0.50%
Max. salt	0.60%
Max. fluoride	0.01%
Min. phosphorus from bone	0.80%
Min. calcium from bone	1.00%
Max. calcium from bone	1.25%
Min. vitamin A	15,000 IU/kg
Min. vitamin D3	3,000 IU/kg
Min. vitamin E	44 mg/kg
Min. vitamin B1	2.8 mg/kg
Min. vitamin B2	5.6 mg/kg
Min. vitamin B6	2.8 mg/kg
Pantothenic acid	14.0 mg/kg
Niacin	44.0 mg/kg
Min. vitamin B12	14.0 mcg/kg
Copper (as copper sulphate)	0.00125%
Iron (as ferrous sulphate)	0.0050%
Zinc (as zinc oxide)	0.0055%
Magnesium (as magnesium oxide)	0.0150%
Iodine (as Potassium iodate)	0.00015%
Cobalt (as cobalt oxide)	0.00010%

APPENDIX TWO

Examples of programs for GENSTAT used in data analyses.

2a. Linear regression of estimated percentage food volumes in stomach slides on actual percentage food volumes (Section 2.2.5).

```
'REFE' LINE
'VARI' EST,ACT$30
'READ/PRIN=DM' EST,ACT
'HEADING' Y=''ESTIMATED''
'HEADING' X=''ACTUAL''
'GRAPH/ATY=Y,ATX=X,NRF=40,NCF=61' EST;ACT
'RUN'
   list data....
'EOD'
'CLOSE'
```

2b. Analysis of variance for effect of month and habitat on litter sizes of mice caught in rice and sorghum crops (Section 2.3).

```
'REFE' LITSIZ
'UNITS' $41
'FACT' CROP$2=28(1),13(2)
'FACT' MONTH$3=3(1),17(2),8(3),4(2),9(3)
'READ/P' N
'TERMS' N+CROP*MONTH
'Y' N
'FIT/ANDEV=I'
'ADD' CROP:MONTH
'DROP' CROP
'ADD' CROP
'ADD/PRIN=CAU,ANDEV=T' CROP.MONTH
'RUN'
   list data....
'EOD'
'CLOSE'
```

2c. Analysis of variance for treatment effects on numbers of mice caught in the first field experiment (Section 3.2.4).

```
 1 'REFE' NUMBERS
 2 'UNITS' $11
 3 'NAME' FF=PELLET,WHEAT,GA,UNFED
 4 'FACTOR' FOOD$FF=3(1),2(2),2(3),4(4)
 5 'READ/P' N
 6 'FACTOR' CONT$2=7(1),4(2)
 7 'TERMS' N+CONT+CONT.FOOD
 8 'Y' T
 9 'FIT'
10 'FIT/PRIN=CAU' CONT
11 'ADD' CONT.FOOD;FVAL=F;RES=RES
12 'GRAPH' RES;F
13 'TREAT' CONT/FOOD
14 'ANOVA' N; RES=RES;FVAL=F
15 'GRAPH' RES;F
16 'RUN'
   list data...
14 'EOD'
15 'CLOSE'
16 'STOP'
```

2d. Logistic regression analysis test for treatment effects on on breeding intensity, (r/f) in the first field experiment.

```
 1 'REFE' PROPORTIONS
 2 'UNITS' $11
 3 'NAME' FF=PELLET,WHEAT, GA3, UNFED
 4 'FACTOR' FOOD $FF=3(1),2(2),2(3),4(4)
 5 'READ/P' F,R
 6 'FACTOR' CONT$2=7(1),4(2)
 7 'TERMS' F+CONT+CONT.FOOD
 8 'TREATMENTS' CONT/FOOD
 9 'ANOVA' F;RES=RES;FVAL=F
10 'GRAPH' RES;F
11 'RUN'
   list data...
16 'EOD'
17 'CLOSE'
```

```
18 'STOP'
```

2e. Test for effect of diet on litter size for results of Experiment 4, Section 4.3.

```
'REFE' LITSIZ
'UNITS' $48
'FACT' MEALS$2=12(1,2)2
'FACT' SPROUTS$2=24(1,2)
'READ/P' N
'TREAT' MEAL*SPROUT
'TERMS' N=MEAL*SPROUT .
'Y' N
'FIT/ANDEV=I'
'ADD' MEAL:SPROUT
'DROP' MEAL
'ADD' MEAL
'ADD/PRIN=CAU,ANDEV=T' MEAL.SPROUT
'RUN'
   list data...
'EOD'
'CLOSE'
'STOP'
```

2f. Analysis of variance for treatment effects on numbers of mice caught (n) in the second field experiment (Chapter 5).

```
'REFE' NUMBERS
'UNITS' $16
'FACTOR' FARM$2=8(1,2)
'FACTOR' FOOD$2=4(1,2)2
'FACTOR' CULL$2=2(1,2)4
'READ/P' N
'TERMS' N+FARM+FOOD*CULL
'Y' N
'FIT/ANDEV=I'
'ADD' FARM
'ADD' FOOD
'ADD' CULL                    ....gives culleffect, adjusted for food
'DROP' FOOD                   ....gives food effect, adjustedfor cull
'ADD/ANDEV=T,PRIN=CAU' FOOD.CULL     ....gives food x cull effect
'RUN'
   data list...
'EOD'
'CLOSE'
```

```
'STOP'
```

2g. Logistic regression analysis for treatment effects on the proportion of breeding females in the adult female mice caught (r/f) in the second field experiment (Chapter 5).

```
'REFE' PROPORTIONS
'UNITS' $16
'FACTOR' FARM$2=8(1,2)
'FACTOR' FOOD$2=4(1,2)2
'FACTOR' CULL$2=2(1,2)4
'READ/P' N,B
'TERMS/TOTAL=N' B+FARM+FOOD*CULL
'Y' B
'Y/ERROR=BINOMIAL' B
'FIT/ANDEV=I'
'ADD' FARM
'ADD' FOOD
'ADD' CULL                ....gives cull effect, adjusted for food
'DROP' FOOD               ....gives food effect, adjustedfor cull
'ADD/ANDEV=T,PRIN=CAU' FOOD,CULL
'RUN'
'EOD'
'CLOSE'
'STOP'
```

2h. Analysis of co-variance.

```
'REFE' CVAR
'UNITS' $385
'READ/P' W,L
'CALC' W=W*0.1
'CALC' LOGW=LOG(W)
'CALC' LOGL=LOG(L)
'HEAD'Y=''LOG WEIGHT''
'HEAD'X=''LOG LENGTH''
GRAPH/ATY=Y,ATX=X,NRF=40,NCF=61' LOGW;LOGL
'NAMES' FA=ONE,TWO
'FACT' FARM$FA=199(1),186(2)
'NAMES' FF=S,R
'FACT' FOOD4FF=89(1),110(2),102(1),83(4)
'NAMES' CC=C,N
'FACT' CULL$CC=36(1),53(2),57(1),53(2),53(1),50(2),44(1),39(2)
```

```
'BLOCKS' FARM
'TREAT' FOOD*CULL
'COVAR' LOGL
'ANOVA/SE=M' LOGW
'RUN'
   read in data...
'EOD'
'CLOSE'
'STOP'
```

APPENDIX THREE

Data for instantaneous rates of decline (IRD) for females initially caught in trap-session T1 in the second field experiment (see Section 5.2.7 for method of calculation and Section 5.3.3 for results of analysis for treatment effects).

Food	High-quality food				Low-quality food			
Culling	Culled		Unculled		Culled		Unculled	
Farm / Period	one	two	one	two	one	two	one	two
P1	0.0317	0.0242	0.0000	0.1425	0.1221	0.0742	0.1014	0.0327
	0.0353	0.0937	0.0576	0.1332	0.0531	0.0797	0.0707	0.0680
P2	0.0989	0.1099	0.1052	0.1099	0.1052	0.0805	0.1228	0.0973
	0.0805	0.1282	0.1052	0.1168	0.1857	0.1282	0.1099	0.1568
P3	0.0911	0.0978	0.1297	0.1334	0.1258	0.1963	0.1939	0.1073
	0.1374	0.1512	0.1377	0.0849	0.2030	0.1156	0.0905	0.0849
P4	0.0684	0.0437	0.0847	0.0803	0.0401	0.0415	0.0578	0.0578
	0.0503	0.1262	0.0557	0.0748	0.1024	0.0847	0.0925	0.0651