

Food and Reproduction of Wild House Mice

I. Diet and Breeding Seasons in Various Habitats on Irrigated Cereal Farms in New South Wales

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Abstract

The diet and breeding seasons of house mice, *Mus musculus* L., were monitored for 16 months in six habitats on two cereal farms: fields of barley, wheat, sorghum and rice stubble, and contour banks in rice fields, and channel banks. In all habitats mice were mainly granivorous. Because of rotational cropping and irrigation, seeds were available in different habitats in each season and this was reflected in the diets. Cereal grains spilt at harvest and other stale seeds were the main food in the nonbreeding season. It is proposed that the low quality of this food limited breeding. When milk-ripe grass seeds became available, mice switched to this fresh food, and started breeding about 1 month later. The onset of breeding was asynchronous between different habitats; this suggests that time of onset of breeding was determined by availability of food.

Introduction

This is the first in a series of publications on the relationship between food quality, food availability, and reproduction of the house mouse on irrigated cereal farms in the Murrumbidgee Irrigation Region (M.I.R.) of New South Wales.

The reproductive performance of house mice is affected by either the quality or the abundance of available food (Strecker and Emlen 1953; Newsome 1970; Bronson 1979; Pryor and Bronson 1981; Ward 1981; King 1982; Redhead 1982), by temperature (Pennycuik 1972a, 1972b, 1973; Barnett *et al.* 1975; Bronson 1979; Pryor and Bronson 1981) and by social effects (Lidicker 1965, 1976; DeLong 1967, 1978; Vandenberg *et al.* 1972). In commensal populations (in buildings, grain stores, haystacks and ricks, food stores, and bird enclosures) where food supplies are relatively constant, breeding usually occurs 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 (on both cultivated and uncultivated land) usually cease breeding for at least 4 months in winter (Naumov 1940; Breakey 1963; Lidicker 1966; Newsome 1969a, 1969b; Stickel 1979; Smiet *et al.* 1980; Pelikan 1981). I have found only four records of winter breeding in wild mice, and each of these corresponded with an unusual abundance of winter food, which resulted either from supplementary feeding (DeLong 1967; Newsome 1970), or from an exceptionally abundant or prolonged yield of natural seed (King 1982; Redhead 1982). Bronson (1979) reviewed the environmental factors likely to cause cessation of breeding during winter, and concluded that temperature, variation in caloric intake, and variation in the availability of specific nutrients are the most likely factors. He dismissed photoperiod as unimportant, and a later study by Pryor and Bronson (1981) supports this conclusion. Bronson suggested that the separate roles of these factors could never be established in a natural population because all change simultaneously with season; but he thought the diet's energy content was more likely than its nutrient quality to be important in causing seasonal breeding. A later study, however, on caged mice fed different natural diets indicated that diet quality was also likely to be an important factor (Pryor and Bronson 1981).

Seventeen previous studies of natural diets of mice in the field were examined by Bomford (1985). Seeds were the main food in all nine studies conducted in cultivated habitats (Naumov 1940; Sakhno 1957; Hamar 1960; Kami 1966; Whitaker 1966; Mikes 1971; Houtcooper 1978; Smiet *et al.* 1980; Fulk *et al.* 1981), but there was more variation in studies in uncultivated habitats, with animal tissue the main food in three (Watts and Braithwaite 1978; Cockburn 1980; Gleeson 1981), seeds the main food in three (Caldwell 1964; Watts 1970; Thomson 1979), and both plant and animal foods recorded in two, although the relative amounts were not given (Berry 1968; Berry and Tricker 1969). Animal foods were mainly insects (especially larvae) but other invertebrates, feathers and vertebrate flesh were also recorded. Non-seed plant tissue included leaf, root and stem tissue, and less frequently fruit or fungus. Variation in relative amounts of plant and animal tissue recorded probably reflects both availability of foods in the different habitats and different techniques used to analyse the diets. Although there were obvious seasonal changes in the proportions of plant and animal foods found in many of the studies, there were no consistent seasonal trends.

In none of the 17 studies were both diet and breeding monitored simultaneously, and in sufficient detail, to determine whether dietary inadequacies curtailed or inhibited breeding.

This paper presents results from a study of the diet and breeding of mice in six habitats on cereal farms in the M.I.R. Here, rotational cropping is practised, with wheat and barley being grown in winter and harvested in late spring, and sorghum and rice being grown in summer and harvested in autumn. Hence, in a given month, the type and abundance of food in any field vary according to the crop grown and its maturity. This means that mice in different fields are exposed to different food conditions but to the same ambient temperatures. Therefore, if breeding is limited by low temperature, it should decline in all fields simultaneously when temperatures drop in autumn. If, on the other hand, breeding is limited by food availability, its intensity should decline after harvest when grain supplies become depleted; this would be in midsummer in wheat and barley fields, but not until late autumn in rice and sorghum fields. If food quality limits breeding, correlations would be expected between food types in the diet, and timing of breeding. Thus this situation provides an opportunity to examine separately the relative roles of food availability, food quality and temperature in producing seasonality of breeding. Bronson (1979) suggested that such an opportunity would not exist for natural populations of house mice.

Methods

Study Site

The study was conducted on two neighbouring farms (farms 25D and 25H) in the Benerembah district, 20 km south-west of Griffith, N.S.W. (34°17'S., 146°2'E.) in the M.I.R.

Total rainfall for Griffith in 1979 was 299 mm and for the first four months of 1980 was 83 mm. Summers in both years were dry, with an average of only 5.0 mm of rain in each summer month. In the summer months maximum mean weekly temperatures ranged from 27.8 to 45.4°C, and mean minima from 11.7 to 21.5°C. In the winter months maximum mean weekly temperatures ranged from 13.9 to 18.8°C and mean minima from 0.9 to 7.4°C. There were occasional winter frosts.

The fields in which crops are grown consist of a series of bays, separated by low contour banks about 0.5 m high, which regulate the levels of irrigation water. Irrigation water is distributed throughout the farms by a series of open channels. The banks of these channels support a prolific growth of wild grasses and forbs.

During the study period, two winter crops were grown on the study farms: wheat (60 ha sown June, harvested November); two-row barley (50 ha sown June, harvested November). Two summer crops were grown: rice (two 80-ha fields, each sown late September and early October, harvested late March); sorghum (45 ha sown late October, harvested June). After harvest, the stubble was left fallow in all fields, but the barley and wheat stubbles were grazed by sheep, and the wheat stubble was aerially sown with clover seed in early April.

Seed Nitrogen Assays

Some seeds collected from habitats where traps were set were assayed for nitrogen content, by the method of Williams and Twine (1967), so that their protein content could be estimated.

Collection of Mice

Trapping with break-back traps was conducted in six habitats: wheat field, barley field, rice field contour banks, rice stubble bays, sorghum fields, and channel banks. All trapping was conducted between January 1979 and April 1980. In cereal crops, trapping started 3–5 months before harvest, and continued, at approximately monthly intervals, for up to 9 months after harvest. On channel banks, trapping was conducted for 1 year. Traps were laid in lines of 50, with single traps placed at 8-m intervals. Bait was a small piece of leather soaked with linseed oil. This bait was not swallowed by the mice and so did not contaminate the stomach contents.

Breeding Intensity and Litter Size

The uteri of adult females were examined macroscopically for embryos. The percentage of adult females which were visibly pregnant was used as a measure of breeding intensity. Mean litter size was measured by counting the embryos (not including any which were clearly undersized and underdeveloped compared to their siblings).

Stomach Content Analyses

There are problems associated with methods used previously for identification and quantification of house mouse diet by either faecal or stomach content analyses (Hansson 1970; Neal *et al.* 1974). They were considered unsuitable for use in the present study for the following reasons.

- (1) The identification of material in faecal samples was found to be difficult.
- (2) Faecal analyses may 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.
- (3) Washing and sieving of samples, to obtain a uniform particle size, leads to a biased loss of foods, particularly starchy endosperm, the major food of mice. Also, this loss from the small volume of material usually available from mouse stomachs may leave a sample too small for preparation of microscope slides.
- (4) The use of counts of surface areas of fragments, or point counts of particles present on a grid, are methods developed for quantifying herbivore diets, and their accuracy depends on the assumption that food items have relatively uniform thickness, as do leaves. Foods eaten by house mice are irregular in shape and thickness, so that this assumption does not hold.

(5) The visual identification and quantification of stomach contents spread in a dish (e.g. Sakhno 1957; Houtcooper 1978; Thomson 1979; Gleeson 1981) was not possible in the present study because stomach contents were usually a finely ground homogenous paste with different foods mixed together.

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. The following method, used to identify and quantify stomach contents in the present study, is described in more detail in Bomford (1985).

Only stomachs containing at least 0.3 ml of food were used. The stomach contents were thoroughly mixed in a dish, and then samples were taken to prepare two microscope slides from each stomach. The first slide was made from a sample of untreated stomach contents. The second slide was made from a sample that had been incubated for 10 min in a dilute solution of nitric and chromic acids by Fitzgerald's (1976) method, but with only half the acid concentrations specified. This acid treatment dissolved starch granules and other amorphous material, and left fragments of seed coat clearly visible. Each sample was stirred into a drop of glycerine jelly on a microscope slide, covered with a 22 by 50-mm coverslip pressed down firmly to remove air bubbles, and sealed with nail varnish. No staining was used, but slides were observed under polarised light, which enhanced contrasts between different foods.

Identification of seeds in stomachs was further aided by the use of reference slides. In each trap-session the plants and ground in each habitat were searched for seeds. These were identified, mainly by reference to Cunningham *et al.* (1982), and lists were made of all seeds found. A sample of each seed type was collected and fed to a caged mouse for 48 h, after which the mouse's stomach contained only this seed. The stomach contents were then used to prepare an untreated and an acid-treated slide by the above method. Monocotyledon seeds were identified mainly from the shape, size and cluster pattern of starch granules from the endosperm in slides of untreated stomach contents, but when this was insufficiently distinct to allow definite identification, the appearance of seed coat fragments in acid-treated slides was also used. Other seeds, especially oilseeds and other non-starchy dicotyledon seeds, were mostly identified from seed coat fragments, because cotyledon tissue usually showed no distinctive

characters. Although mice generally husked all but the smallest seeds, fragments of seed coat were swallowed, especially the inner layers. Seeds were the major food, and all the main seeds eaten were identified to species. Some of the seeds which occurred less frequently were not identified, and were only classified as grass seeds, or as starchy or non-starchy dicotyledon seeds. Other foods were classified as non-seed plant tissue (mainly green leaf and stem tissue), or as invertebrate. A further category was grit, which appeared in small quantities in many stomachs. A few stomachs contained mouse flesh and fur, but because this was only present when chewed mice had been recorded in the traps, such a food source was considered unnatural, and these stomachs were rejected.

Stomach contents were quantified only from slides of untreated stomach contents. After the foods present were identified, 20 systematically spaced fields-of-view (FOV) were examined under 40 \times magnification. In each FOV the percentage volume contributed by each food was visually estimated; the sum of all foods in each FOV totalled 100%. The mean percentage value for each food for the 20 FOVs was taken as the volume of that food in the stomach.

This method of quantifying food, although subjective, was tested for accuracy and found to be well within acceptable limits for the purposes of this study. Details of these tests are present in Bomford (1985). The main source of uncertainty in volume estimates was not the errors introduced by the method of analysis, but the small sample sizes on which the means were based. With the formula given by Hanson and Graybill (1956), it was calculated that in some months and habitats, when the diet was highly varied, a sample of more than 100 stomachs would have been required for the mean volume estimate for the main food eaten to have a confidence interval of less than 10%. Because the mean sample size was only eight, confidence intervals were often much wider, so that all estimates for volumes of the main food eaten are given with a standard error.

Results

Available Seeds

In late winter and early spring, seeds were scarce in all habitats, being only weed seeds left from the previous season, and small quantities of ungerminated grain from previous crops or from sowing.

In wheat and barley fields and on channel banks, irrigation during winter and early spring promoted the growth of several grass species, and the seeds of these grasses reached the milk-ripe* stage in early September. This caused the food supply to change from scarce to abundant in just a few days. The first species to become milk-ripe was barley grass *Hordeum leporinum* L., followed about 3 weeks later by rye grass *Lolium rigidum* Gaudin, and phalaris *Phalaris aquatica* L. Wheat and barley grain became milk-ripe in October. In the rice and sorghum fields, irrigation water was not applied until October, and consequently only a few plants of the above grass species grew in these fields. Sown grain was the only other food source for mice during spring in these summer crops. It was not until early January, when barnyard grass *Echinochloa crus-galli* L. became milk-ripe, that food became abundant in these habitats. Hence in rice and sorghum fields, fresh grass seeds did not become abundant until 3–5 months later than in wheat and barley fields. Rice and sorghum grain became milk-ripe in early March.

Grain spilt at harvest, up to 1 tonne per hectare in rice fields, provided plentiful food for at least 1 month, before foraging mice, ants and birds depleted supplies. Dicotyledon weeds that seeded in summer and autumn provided a further source of food in stubble fields, on contour banks and on channel banks.

Diet

The results of the stomach content analyses are presented in Fig. 1 and Table 1. Seeds were the main food in all habitats and in all months. Seed species identified in the stomachs of wild-caught mice are listed below.

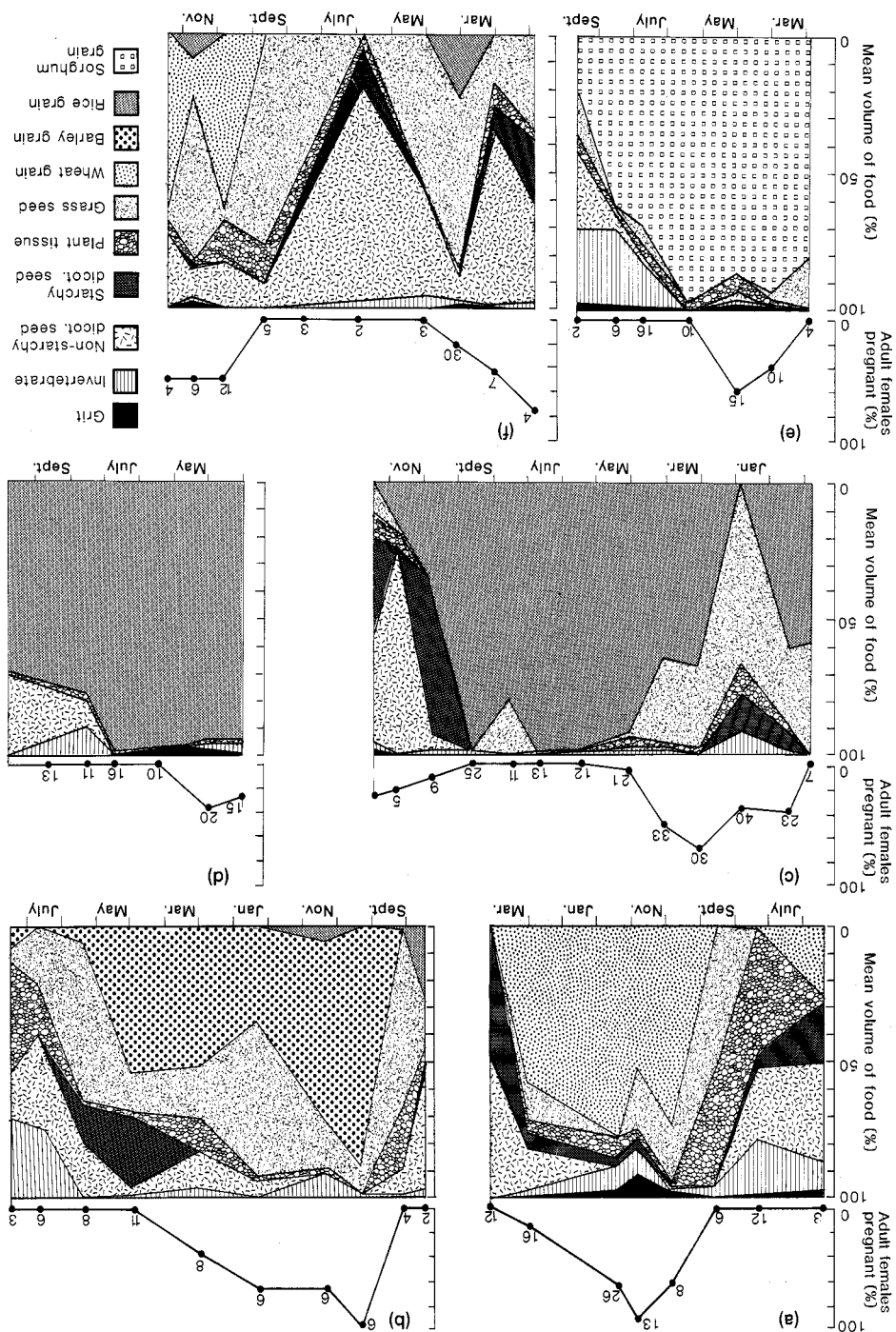
*Milk-ripe seeds are full-sized or nearly so, and their endosperm contains starch granules; but they are still green, and if squeezed exude a 'milky' juice.

Table 1. The main foods eaten by mice in each month, in each habitat

N, number of mice. Food volume expressed as mean (\pm standard error) percentage volume of total stomach contents

Habitat	Month	<i>N</i>	Main food	Food volume
Wheat crop	June	6	Dicotyledon seeds	36.3 \pm 18.7
	Aug.	12	Non-seed plant tissue	45.6 \pm 11.3
	Sept.	6	Barley grass seed	52.6 \pm 16.4
	Oct.	8	Wheat grain	73.2 \pm 13.6
	Nov.	18	Wheat grain	52.5 \pm 8.6
Wheat stubble	Dec.	12	Wheat grain	77.9 \pm 10.2
	Feb.	5	Wheat grain	58.1 \pm 14.8
	Apr.	6	Wireweed	46.8 \pm 13.4
Barley crop	Aug.	6	Non-starchy dicotyledon seed	39.6 \pm 13.7
	Sept.	7	Barley grass seed	64.6 \pm 11.9
	Oct.	6	Barley grain	88.2 \pm 6.7
	Nov.	9	Barley grain	66.7 \pm 10.6
Barley stubble	Jan.	10	<i>Phalaris</i> seed	57.0 \pm 8.9
	Feb.	6	Barley grass seed	52.1 \pm 16.0
	May	7	Barley grain	54.6 \pm 17.4
	June	7	Grass seed	58.3 \pm 14.2
	July	10	Invertebrate	23.5 \pm 8.8
	Aug.	4	Non-seed plant tissue	26.6 \pm 15.4
	Nov.	5	Rice grain	59.2 \pm 24.2
	Dec.	6	Rice grain	61.1 \pm 19.5
Rice field contour bank	Jan.	4	Grass seed	66.1 \pm 19.5
	Feb.	6	Rice grain	67.6 \pm 16.4
	Apr.	26	Rice grain	64.2 \pm 7.0
	May	9	Rice grain	91.8 \pm 3.0
	June	8	Rice grain	98.4 \pm 0.8
	July	8	Rice grain	98.8 \pm 0.6
	Aug.	3	Rice grain	79.6 \pm 19.9
	Sept.	6	Rice grain	98.7 \pm 0.4
	Oct.	7	Starchy dicotyledon seed	57.5 \pm 16.3
	Nov.	6	Non-starchy dicotyledon seed	75.7 \pm 2.7
	Dec.	8	Non-starchy dicotyledon seed	39.5 \pm 13.6
Rice stubble	Apr.	21	Rice grain	94.3 \pm 1.7
	May	6	Rice grain	94.2 \pm 1.8
	June	6	Rice grain	96.9 \pm 2.1
	July	7	Rice grain	98.2 \pm 0.6
	Aug.	6	Rice grain	77.3 \pm 7.0
	Oct.	4	Rice grain	69.0 \pm 23.1
	Feb.	4	Sorghum grain	79.9 \pm 10.6
Sorghum crop	Apr.	15	Sorghum grain	92.9 \pm 1.9
	May	11	Sorghum grain	86.3 \pm 3.4
Sorghum stubble	June	6	Sorghum grain	97.3 \pm 1.6
	July	11	Sorghum grain	70.4 \pm 7.6
	Aug.	6	Sorghum grain	64.3 \pm 10.9
	Sept.	4	Invertebrate	28.1 \pm 11.0
Channel bank	Jan.	6	Grass seed	35.5 \pm 16.9
	Mar.	12	Non-starchy dicotyledon seed	51.2 \pm 11.1
	Apr.	6	Grass seed	62.1 \pm 15.8
	May	6	Non-starchy dicotyledon seed	39.3 \pm 13.1
	June	5	Non-starchy dicotyledon seed	78.0 \pm 14.0
	Sept.	6	Grass seed	76.6 \pm 10.4
	Oct.	8	Grass seed	63.7 \pm 17.0
	Nov.	10	Grass seed	59.1 \pm 13.4
	Dec.	6	Grass seed	64.0 \pm 20.3

Fig. 1. Breeding and diet of mice in: (a) wheat field; (b) barley field; (c) rice field contour banks; (d) rice stubble field; (e) sorghum field; (f) channel banks. Adult female sample sizes beside points.



Monocotyledons

Two row barley, *Hordeum distichon* L.
 Barley grass, *Hordeum leporinum* Link
 Barnyard grass, *Echinochloa crus-galli* (L.)
 Awnless barnyard grass, *Echinochloa colona* (L.)
 Maize, *Zea mays* L.
 Narrowleaf cumbungi, *Typha domingensis* Pers.
 Common oats, *Avena sativa* L.
 Phalaris, *Phalaris aquatica* L.
 Paradoxa grass, *Phalaris paradoxa* L.
 Rice, *Oryza sativa* L.
 Annual ryegrass, *Lolium rigidum* Gaudin
 Forage sorghum, *Sorghum bicolor* (L.)
 Wheat, *Triticum aestivum* L.
 Wild oats, *Avena fatua* L.

Non-starchy dicotyledons

Black berry nightshade, *Solanum nigrum* L.
 Burr medic, *Medicago polymorpha* L.
 Capeweed, *Arctotheca calendula* (L.)
 Paterson's curse, *Echium plantagineum* L.
 Common peppergrass,
Lepidium hyssopifolium Desv.
 Quena, *Solanum esuriale* Lindl.
 Saffron thistle, *Carthamus lanatus* L.
 Spear thistle, *Cirsium vulgare* (Savi)
 Subterranean clover, *Trifolium subterraneum* L.
 Sunflower, *Helianthus annuus* L.
 Native bluebell, *Wahlenbergia communis* Carolin
 Variegated thistle, *Silybum marianum* (L.)
 Yellow wood sorrel, *Oxalis corniculata* L.

Starchy dicotyledons

Curled dock, *Rumex crispus* L.
 Shiny dock, *Rumex tenax* Rech.f.
 Wireweed, *Polygonum aviculare* L.

Many additional seed species found in habitats where traps were set were eaten readily by caged wild mice, but were not identified in the stomachs of wild-caught mice. These species are listed below.

Monocotyledons

Great brome *Bromus diandrus* Roth
 Neverfail grass *Eragrostis setifolia* Nees
 Pale pigeon grass *Setaria pumila* (Poir.)
 Prairie grass *Bromus unioloides* Kunth
 Soft brome *Bromus molliformis* Lloyd

Starchy dicotyledons

Shiny dock *Rumex crystallinus* Lange

Non-starchy dicotyledons

Australian carrot *Daucus glochidiatus* (Labill.)
 Bushy starwort *Aster subulatus* Michx.
 Barrel medic *Medicago truncatula* Gaertn.
 Bathurst burr *Xanthium spinosum* L.
 Creeping saltbush *Atriplex semibaccata* R.Br.
 Common heliotrope *Heliotropium europaeum* L.
 Dandelion *Taraxacum officinale* Wiggers
 Horehound *Marrubium vulgare* L.
 Lucerne *Medicago sativa* L.
 Prickly paddy melon
Cucumis myriocarpus Naudin
 Salsify *Tragopogon porrifolius* L.
 Wild sage *Salvia verbenaca* L.

The diet closely reflected available foods in each season and habitat. The time when grass seeds became available and were included in the diet varied by as much as 5 months between habitats. When cereal grains ripened, they immediately became the main food, and remained so for as long as 7 months. Non-seed plant tissue, mainly green leaf and stem tissue, was present in 71% of the stomachs examined, and when present, averaged 7.7% of the total content. It was found in large quantities in the diet only in the wheat field before grass seeds ripened, when seeds were scarce. Invertebrate tissue was found in 39% of stomachs, and where present, averaged 9.4% of the total content. It was present in some stomachs from all habitats, and consisted mainly of insects, with lepidopteran larvae particularly well represented. There were no apparent seasonal trends in the occurrence of invertebrate food in the diet; it was present in large quantities only in the sorghum stubble field during August and September, when grain supplies were almost exhausted and the mice were eating mainly earthworms (present in large numbers under the piles of decomposing stubble.)

The protein content of barley grass seeds (21.0%), which grew in wheat and barley fields, was much higher than that of wheat grain (13.2%) or barley grain (12.6%). Similarly,

the protein content of barnyard grass (13.9%), which grew in rice and sorghum fields, was higher than that of rice grain (7.2–9.0%) or sorghum grain (9.9%).

Breeding Intensity

Breeding in wheat and barley fields (Figs 1a, 1b) started in October. In contrast, breeding did not start in rice fields until December (Fig. 1c), and not until March in sorghum fields (Fig. 1e). The common factor in all habitats was that breeding started about 1 month after milk-ripe grass seeds became available, and this occurred as much as 5 months apart in different fields. Breeding intensity peaked around the time cereal crops ripened, and thereafter declined. Hence breeding was asynchronous between different fields, and the breeding seasons in the wheat and sorghum fields did not overlap.

Table 2. Mean (\pm standard error) litter sizes of mice in various habitats, at various times

Values in parentheses are sample sizes

Day + month	Wheat field	Barley field	Rice field	Sorghum field	Channel bank
25 Jan.		7.3 \pm 0.8 (3)			6.3 \pm 0.6 (3)
28 Feb.		6.0 \pm 0.6 (3)	8.7 \pm 0.9 (3)		7.3 \pm 0.4 (3)
1 Apr.			7.8 \pm 0.7 (17)	6.5 \pm 0.3 (4)	3 (1)
1 May			7.0 \pm 1.0 (8)	4.7 \pm 0.5 (9)	
23 Oct.	8.6 \pm 0.2 (5)	7.8 \pm 0.3 (6)	5 (1)		7.3 \pm 0.6 (6)
20 Nov.	8.3 \pm 0.5 (15)		6 (1)		8.7 \pm 0.4 (3)
12 Dec.	7.1 \pm 0.4 (16)		6.5 \pm 0.3 (4)		8.0 \pm 1.0 (2)

No breeding was recorded in the four coolest months from June to September, when mean minimum temperatures for the week preceding each trap-session were below 8°C. There was no indication of correlation between temperature and breeding intensity in other months.

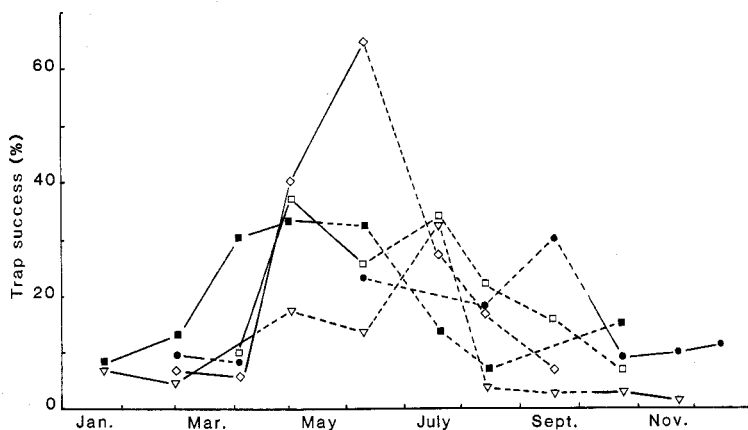


Fig. 2. Percentage trap success (average number of mice caught in 100 traps in one night) during the breeding season (—) and the non-breeding season (---) in various habitats: ■ rice contour bank; ◇ sorghum; □ rice stubble; ● wheat; ▽ barley.

Litter Sizes

Data on litter sizes are presented in Table 2. A total of 108 litters were counted, and the overall mean (\pm standard error) litter size was 7.29 ± 0.20 . There were no clear patterns in litter size variations.

Numbers

Data for numbers of mice trapped are presented in Fig. 2. Numbers of mice stayed fairly low in wheat and barley fields throughout the breeding season. In contrast, there were large numbers of mice in rice and sorghum fields in the later part of the breeding season and early non-breeding season.

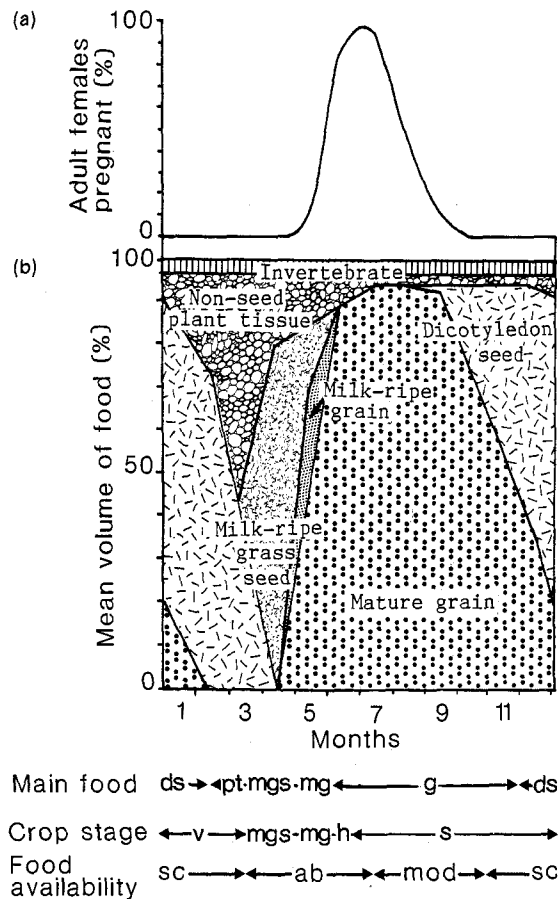


Fig. 3. Model of changes in breeding (a) and diet (b) in relation to the stages of crop growth and harvest. Breeding can start in any month from October to March. Food symbols: *ds*, dicotyledon seed; *pt*, non-seed plant tissue; *mgs*, milk-ripe grass seed; *mg*, milk-ripe grain; *g*, mature grain. Crop stage symbols: *v*, vegetative; *mgs*, milk-ripe grass seed; *mg*, milk-ripe grain; *h*, harvest; *s*, stubble. Food availability symbols: *sc*, scarce; *ab*, abundant; *mod*, moderate.

Discussion

The main finding of this study is the apparent link between food availability or food quality, and timing of breeding. Breeding did not start in any habitat until after fresh milk-ripe grass seeds became available, and this happened up to 5 months apart in different fields. Thus there was a clear link between the time when fresh grass seeds and cereal grain first became available, and the times when breeding began and peaked. A model of this apparent relationship is presented in Fig. 3.

Peak breeding in all fields occurred when fresh cereal grain became available. Breeding intensity declined immediately after harvest, when grain was still abundant. Breeding could have ceased or been below maximum intensity because of dietary inadequacies in: (1) energy;

(2) specific nutrients; (3) chemical breeding stimulants. These factors are now discussed briefly.

(1) *Energy*. Breeding declined in crop fields immediately after harvest, when there was still an abundant supply of spilt grain, the main food of the mice; thus energy clearly was not undersupplied at these times. But by midwinter food supplies of grain and seeds on the soil surface were largely depleted. Although McIntyre (1983) reported that soils in rice stubble fields contain a diverse and often abundant seed bank, and found that the soils of rice field contour banks contained 77–6400 seeds per square metre, it is doubtful whether or not underground seeds were a good food source; grass seeds rarely appeared in the mouse diet when they were not freely available above ground. Further, whereas *Mus hortulanus* and *Mus molossinus* apparently hoard food (Naumov 1940; Hamar 1960; Hamajima 1962), this activity has not been reported for *Mus musculus*, and no food hoards were found on M.I.R. farms even though 12 burrow systems were dug up in midwinter in a search for underground stores. Therefore, until fresh seeds become available in the following spring or summer, it is likely that the energy supply may limit breeding.

(2) *Nutrients*. Mature grain is low in some vitamins, and rice grain contains negligible quantities of vitamins A and D (Grist 1975). Even B-complex vitamins, which are well supplied in fresh grain, may deteriorate in grain which is exposed to water and sunlight. The protein content of grains, especially rice grain, is low and of poor quality (Food and Agriculture Organization 1970), and the breeding performance of caged mice fed diets low in protein may be impaired and onset of sexual maturity delayed (Vandenbergh *et al.* 1972; Knapka 1983). Hence protein may have been a limiting nutrient for breeding when mice were eating grain. Because grass seeds have a higher protein content than cereal grains, the large quantities of grass seeds eaten by mice just before the start of the breeding season may be an important source of dietary protein, which may affect the time of onset of breeding.

(3) *Chemical cues*. It is frequently suggested that breeding in small mammals is cued or stimulated by chemicals present in green food but absent from dried-out mature food (Bradbury 1944; Negus and Berger 1977; Negus *et al.* 1977; Lam 1983; Alibhai 1985). One such chemical is 6-methoxybenzoxalnone, which stimulates breeding in *Microtus montanus* (Peale), (Negus and Pinter 1966; Berger *et al.* 1981; Sanders *et al.* 1981), and an increase in ovarian weight of albino mice (Sanders *et al.* 1981). However, Rose *et al.* (1982) found that this chemical did not affect the breeding performance of field populations of house mice. Another chemical, the plant growth hormone gibberellin- A_3 (GA_3), when added to drinking water in concentrations between $10^{-4}M$ and $10^{-7}M$, was found by Olsen (1981) to stimulate breeding in caged wild-strain mice collected from the M.I.R. These levels of GA_3 or related compounds with similar activity are found in milk-ripe grass seeds and cereal grains, but in mature seeds and grains are bound in inactive forms or are absent (Murakami 1960; Stoddart 1965; Osasda *et al.* 1973; Kurogochi *et al.* 1979). Hence a possible causal link exists between milk-ripe seeds in the diet, and the time of onset of breeding.

The failure of mice to breed in any habitat during the four coldest months may indicate that low temperatures were inhibiting breeding, but the poor food supplies in those months may also have played a role. In other months it is clear the breeding was not limited by temperature. Pryor and Bronson (1981) suggest that low temperatures and inadequate food supplies act together to suppress breeding in winter.

It is more difficult to determine whether or not social factors played a role in the regulation of breeding, because it is uncertain how they operate in natural populations (Bronson 1979). But experiments with enclosed populations indicate that, when numbers are high, social suppression of breeding occurs (Southwick 1958; Rowe *et al.* 1964; Lloyd and Christian 1969; DeLong 1978). In wheat and barley fields, numbers remained low throughout the breeding season, so that it is unlikely that social suppression of breeding was

important. In contrast, numbers were high in rice and sorghum crops during autumn and early winter, so that it is possible that the autumn decline of breeding in these habitats was caused, at least in part, by social factors. Redhead (1982) suggests that both declining food quality and increasing population density play a role in suppressing breeding in rice fields during winter, and this possibility clearly requires further investigation.

Although mean litter sizes varied considerably between habitats in some months, the cause is not clear because no consistent pattern is obvious. Many factors could have been responsible, such as parity and age effects, variable abundance or quality of food, and occasional small sample sizes. Redhead (1982) suggests that even small differences in mean litter sizes could have important demographic consequences, and he thinks that the annual change in this parameter is one of the factors which determines when house mouse plagues occur in the M.I.R. Hence there is clearly a need for more data to be collected so that the causes of variations in litter size can be identified.

These conclusions conform to Bronson's (1979) view that seasonality of breeding is caused by seasonal changes in food availability, and support suggestions that food quality, the temperature, and social factors may also be important (Pryor and Bronson 1981; Ward 1981; Redhead 1982). The role of these factors in limiting breeding is examined in two field experiments described in later papers (Bomford 1987a; Bomford and Redhead 1987) and a series of experiments conducted on caged mice (Bomford 1987b).

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