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Is reproduction of the Australian house mouse (*Mus domesticus*) constrained by food? A large-scale field experiment

Abstract Food quantity and especially food quality are thought to be key factors driving reproductive changes in the house mouse, *Mus domesticus*, leading to outbreaks of house mouse populations in the Australian grain-growing region. Characteristic changes during an incipient mouse plague are an early start of breeding, a high proportion of females breeding at a young age and a prolonged breeding season. We conducted a large-scale food manipulation during an incipient mouse plague, which started with early breeding and relatively high spring numbers of mice. We measured background food availability in four farms throughout the study and conducted a food manipulation experiment from November to March in two of them. After harvest in December 100–200 kg/ha spilled grain remained in the stubble. This was depleted by March. In two treatment farms we added high-protein food pellets on a weekly basis between November and March and two farms served as controls. We measured changes in mouse numbers by capture-mark-recapture trappings and changes in reproduction by scoring embryos and recent placental scars at necropsy. Mouse numbers did not differ between treatments and controls. There were no differences in the litter size or the proportion of females breeding between treatments and controls. We observed the normal pattern of high litter size in spring and decreasing litter size towards the end of summer in treatments and controls. In all farms reproduction stopped in March. Mouse numbers were high but not at plague densities. Contrary to our prediction we did not observe food constraint affecting the reproduction of female mice. Our field experiment seems to rule out food quality as the driving factor for improved reproduction and formation of an outbreak of mice. We suggest that physiological mechanisms in mice might not enable them to take advantage of food with a high protein content in arid summers in southeastern Australian grain fields because of the lack of free-standing water.

Keywords House mouse plague · Reproduction · Food constraint · Water · Supplemental food

Introduction

Limiting food resources has been widely accepted as one of the most important factors affecting life history strategies since Lack (1947), especially in birds (Martin 1987) but also in mammals (Sikes and Ylönen 1998). The relationship between food resources and reproduction has been widely studied in mammals. Positive effects on mice and vole reproduction have been observed during the production of beech or oak mast in European deciduous forests (Jensen 1982; Jedrzejewski and Jedrzejewska 1996; Hansson et al. 2000) or spruce mast in boreal forests (Ylönen and Viitala 1985; Ylönen et al. 1988). Most experimental studies have examined the effect of food addition on population level (reviewed in Boutin 1990; Doonan and Slade 1995; Wauters and Lens 1995; Predavec 2000), with food supplementation advancing the onset of breeding and reproductive success in individual rodents (Duquette and Millar 1996; Koskela et al. 1998; McAdam et al. 1999; Eccard and Ylönen 2001).

Food-driven changes in reproduction, particularly due to low food quality (Singleton et al. 2001), are regarded as an important factor driving changes in house mouse (*Mus domesticus*) numbers producing irregular outbreaks of mice in the grain-growing region of southeastern Australia (Newsome 1969; Newsome and Crowcroft 1971; Bomford 1987b; Redhead et al. 1985; Singleton 1989; Singleton and Redhead 1990). Population outbreaks are followed by a collapse in population numbers and low numbers for several years thereafter. These outbreaks are costly for the agricultural sector (Caughley et al. 1994)

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and make life stressful in rural areas where outbreaks occur.

Prerequisites for an outbreak seem to be an early onset of breeding and an extended breeding season, driven by April–October rainfall (Pech et al. 1999), but not all years with these characteristics produce a plague (Singleton et al. 2001). Characteristic features for house mouse breeding are large litter sizes during early summer when the standing grain is ripening, decrease in litter size towards late summer and density-dependence in body size of breeding females, i.e. only females with large body size breed during high densities of mice. During periods when the density of mice is low females mature with a smaller body size and probably at an earlier age (Singleton et al. 2001).

As not all years with favourable characters produce a plague there are suggestions and some field evidence that changes in food quality and quality of ripening grain could trigger the onset of breeding (Bomford 1987a, 1987b) and govern the length of the breeding season (Bomford and Redhead 1987). Singleton et al. (2001) postulated four factors that could play an important role in influencing patterns of reproductive change in mice: (1) parity of females and age structure of populations, (2) food supply (quality and quantity), (3) adaptive changes in reproductive effort and survival of individuals, and (4) physiological stress during high densities of mice. Based on 19-years data of the Victorian Mallee region of southeastern Australia, they concluded that mice are most likely to track food quality and quantity and adjust their litter size accordingly.

We report on a large-scale field manipulation of the food supply of mice over the breeding season in a year of an incipient mouse plague (Pech et al. 2001). We monitored population numbers and reproduction of mice in six food-manipulated fence line populations on two farms. These were supplemented with ad libitum high-protein pellets between November 2000 and April 2001. Populations in two farms served as controls. We predicted that:

1. If food does not constrain reproduction in the feral house mouse then, during increasing densities, we would not find any differences in reproduction or length of the breeding season between food-supplemented and control farms.
2. If food quality or quantity during increasing densities of mice are a sufficient to generate a mouse plague, then we would expect our food-supplemented populations to have larger litter sizes or a prolonged breeding period during late summer, or both.

Materials and methods

Study area and habitat

The study areas were located within four farms at Walpeup in southeastern Australia (35°08'S, 142°02'E). Trapping of mice was conducted for 3 consecutive nights each month from October 2000 to March 2001 and in June 2001. Grain and sheep were the main commodities, with alternating paddocks of crop, fallow and pasture. Each paddock was fenced, with fence lines accompanied by a relatively undisturbed border of 3–7 m width. The sections of fence lines (300×20 m) used within a farm were located 300–2,500 m from each other. The farms were 5–8 km apart. We considered the mouse populations along these different sections of fence line to be independent.

The soil of the study area was reddish-brown sandy loam. The climate was Mediterranean, with hot dry summers and cool wet winters. During this study, November was mild with cool mornings and warm days of approximately 25°C. During January and February the weather was very hot, with maximum temperatures of 46°C in January and 40°C in February. March was mild, characterised by cold mornings around 10°C and maximum temperatures of approximately 27°C and a few night-time rain showers.

All data were collected in two main habitats: crop/stubble and the fence line between crop and pasture. The crop was mainly wheat, *Triticum aestivum*, the most common crop cultivated in the area, with smaller paddocks of barley on the sandy hilltops of the paddocks. The height of the almost ripe wheat in November was about 90 cm. The height of the stubble after harvest in December was about 40 cm, with patches of high cover due to unharvested tillers and of little cover along tracks from the harvester. The stubble height decreased between January and March due to sheep grazing.

The fence line vegetation consisted of patches of dry weeds, some living plants such as wild melon *Citrullus lanatus*, grasses *Bromus* spp. and dry roly-poly bushes, *Salsola* spp., often caught by the barbed wire of the fences. From January to March, vegetation along fence lines was interspersed with patches of bare sand, creating a habitat mosaic [see Jacob et al. (2003) for details on the vegetation cover along the fence line]. Adjacent pasture had limited complexity, characterised by thin and short vegetation (see Ylönen et al. 2002).

Estimation of food background

Ripening grain in October and November provides shelter and the dominant food for mice. After harvest, spilled grain in the stubble provides the main food source for mice (Tann et al. 1991).

Food quantity

We estimated food quantity each month after harvest from December to March through quadrat sampling of spilt grain. Samples were taken from one of the cropped paddocks in each of the farms adjacent to the regular trapping fence. From each farm thirty 0.1-m^2 quadrats were used to estimate the amount of spilled grain. The samples were distributed evenly in the area between, outside, and in, the tracks left by the wheels of the harvester. If much more chaff seemed to be present in the area between the wheels more samples were taken there (see Jacob et al. 2003 for details). Sampling was conducted along a transect of about 150 m in the paddock. At each sample point, chaff, grain and topsoil to a depth of 2–3 cm were collected and sieved to extract grain. The grain was dried at 50°C for 24 h before being weighed.

Food quality

In November, during the standing crop, we sampled 50 heads of grain from each paddock bordering the fence lines. Two heads were

taken 25 m inside the crop from the fence at 25 sites 10 m apart along a transect of 240 m. The grain was dried at 50°C for 24 h and seeds separated from the heads using a rotary thresher (LD thresher; Wintersteiger, Ried, Austria). Hulls and stems were removed by running the samples through an air seed separator (Saatzucht Laborgeräte, Bad Godesberg, Germany). The resulting cleaned seed material was ground to a fine powder using a rotary puck mill (LM1-P; Lab Technics Australia, Kilkenny) to make an even sample for nitrogen analysis. About 5 mg (exact weight recorded) of the flour was weighed into a tin capsule of known weight and then sealed for analysis. Samples were combusted using the Dumas technique (combustion unit ANCA-NT system; Elworth, UK) and nitrogen (crude protein content as %N) was detected using a Europa 20/20 mass-spectrometer (Europa Science, Elworth, UK).

Food manipulation

High-protein pellet bait was spread on a weekly basis between October 2000 and April 2001, using a commercial bait spreader (Vermeeren, Keith, Australia) that was mounted to a Big Bear 350 four-wheel bike (Hanns, Hume, Australia) and driven at 10 km h^{-1} as close as possible to the fence line. We used dry extruded wheat-based food pellets (Riverina, Yenda, Australia). In October and November we spread pellets that contained soy and wheat as main components (20% protein). From December to April we spread a mixture of two types of pellets, one containing mainly wheat and fish meal and one containing wheat and feather meal (18% protein).

We estimated the amount of supplementary food required by estimating mouse density (Petersen estimate) and assuming a daily rate of consumption of 5 g per day per mouse. Frequent visual estimates verified that pellets were available at all times. We spread approximately 2 kg pellets per fence line each week in October and November and 4 kg per week from December to the end of March. Pellets were spread 1–2 m into the pasture adjacent to the fence, within the uncropped area between the fence and the crop, and up to 12 m into the crop adjacent to the fence.

Selection of farms and estimation of index of population abundance

We trapped mice along one fence line in each farm in September and October to collect baseline data on densities of mice prior to the food addition. The densities were variable between farms and we selected one farm with a high density (adjusted trap success (ATS=79%) and one with a lower density (ATS=27%) as treatment farms and two farms (ATS=78% and 15%) as control farms. Between October 2000 and March 2001 we conducted capture-mark-recapture (CMR) along three fences in each farm and in March and June 2001 along two fences per farm. At the start of the food manipulation 13 fence lines per farm were selected so that where mice were removed was different in each month. This was done to avoid effects of removing mice on the reproduction or densities of mouse populations in the following months.

We trapped mice along three sections of fence line every month. One section was used for 3 consecutive days of CMR within and between months (regular trapping fence), the other two for removal of mice for necropsy after the second night of trapping each month (mice were marked and released on night 1) (= removal fence). In each plot we placed two lines of 20–24 Longworth live traps, one along the fence line and a second line of 20–24 traps in the adjacent crop with a spacing of 10 m between traps. The distance between traplines was 10 m. Traps were baited with wheat, set in the evening and checked shortly after sunrise. Mice were marked with an ear tag or an ear punch upon first capture and released at their point of capture. The mice captured before the removal trappings and from the first day of 3 days of removal trapping were used to calculate ATS (Caughley 1977).

Necropsy data: body size and breeding

Mice were weighed with a spring scale (Pesola, Zurich, Switzerland) and sexed. We measured head-body length of all females and recorded breeding data for females (lactation, number of embryos, number of recent uterine scars). Litter size was based on the number of embryos and the proportion of breeding females was estimated from those females with embryos or recent scars among the adult females (body length >72 mm) in the sample.

Statistical analyses

Repeated measures ANOVA was applied for data analyses between months and treatments if sample size and normality of data allowed it. The quantity of background food between food addition and control areas was analysed using the nonparametric Mann-Whitney test. Proportion of females breeding was analysed with univariate ANOVA. SDs are stated throughout the paper.

We conducted power analyses. The probability to detect a 10% difference in *Mouse numbers* between treatments and controls was 67% and for a 15% difference the power was 95%. The power to detect a 2 mm difference in *Female body size* was 67% and for a 3 mm difference it was 95%. The probability to detect a 1 g difference in body weight was 71% and for 1.5 g it was 96%. There was a high probability to detect a difference in *litter size* of 1 pup (96%) and a difference in *the proportion of breeding females* of 10% (76%) or 15% (97%).

Results

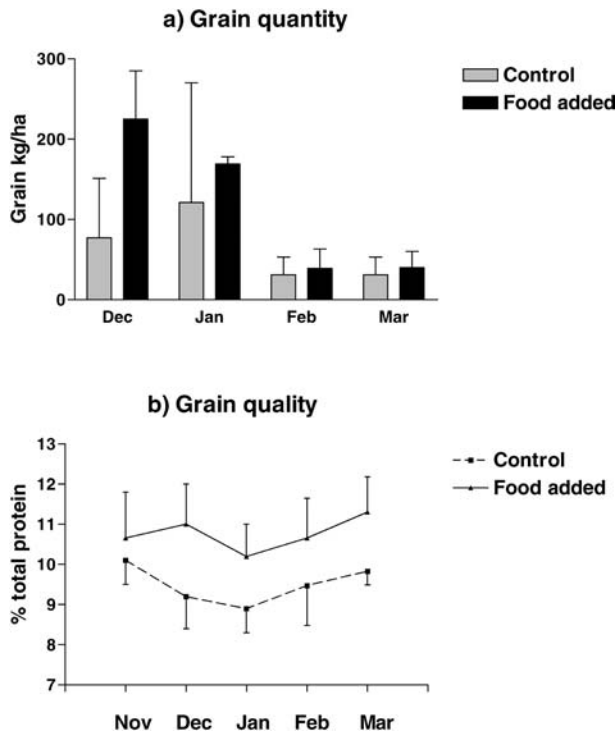## Food background: quality and quantity

The amount of grain left in the fields after harvest ranged from 206±31 kg/ha in December 2000 to 36±10 kg/ha in March 2001. There was high variation in the amount of spilled grain between farms but no significant difference between treatments and controls (Mann-Whitney U-test, two-tailed test, $0.121<P<0.439$ for each month) (Fig. 1A).

The mean protein concentration of grain remained high from the standing crop in November to the spilt-grain sampled 4 months post-harvest in March (range 8.2–11.3% total N between plots and months). Food quality seemed to be consistently higher on the food-addition farms (repeated measures ANOVA, $F=16.88$, $df=1$, $P=0.006$) (Fig. 1B). The pattern of variation was consistent in all months (Wilks' $\lambda=0.340$, $P=0.395$) and in month×treatment interactions (Wilks' $\lambda=0.270$, $P=0.294$).

Mouse numbers

The mouse populations increased markedly from October to June (Fig. 2). Throughout the study there was no difference in adjusted trap success between treatments and controls (Wilks' $\lambda=0.412$, $P=0.138$, month×treatment, Wilks' $\lambda=0.173$, $P=0.008$ [Fig. 2]) and no consistent difference from November to February (repeated measures ANOVA, between subject effect $F=0.637$, $P=0.443$). At the end of the study in June the densities were similar between treatments.

a) Grain quantity

b) Grain quality

Fig. 1a, b Background food quantity and quality. In November (*Nov*) there was standing crop, which was harvested late Nov or early December (*Dec*). **a** Amount of spilled grain after harvest in Dec to March (*Mar*). **b** Protein content of the grain (%N) in heads of standing crop in November and in spilled grain from Dec to Mar. Error bars are SD. *Jan* January, *Feb* February

Mouse numbers 2000 - 2001
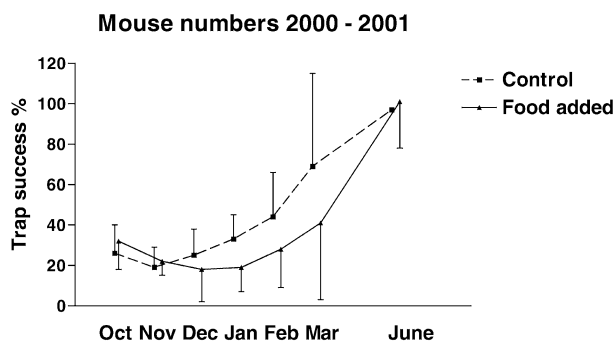
Fig. 2 Mouse (*Mus domesticus*) trap success on treatment and control farms. From October (*Oct*) to Mar the values are an average of six fence lines for food addition and control farms and for Mar and June an average of two fence lines. *Error bars* are SD. Mouse number values for each month are separated by 0.2 units to avoid overlap of SD bars. For other abbreviations, see Fig. 1

Body size of females

There was no difference in body size characteristics between females from food addition farms and control farms throughout the study. On all farms non-pregnant females were heavier in spring at the start of the experiment and lighter in later summer months but with no effect of food addition on these weights (Table 1).

Table 1 ANOVA table for body weight and length of mice (*Mus domesticus*) between food-addition and control farms between November and March

| Accumulated ANOVA				
Change	df	SS	F	P
Ln weight				
Treatment	1	0.10	0.76	0.38
Month	5	2.07	3.25	0.007
Treatment×Month	5	1.43	2.24	0.05
Residual	585	74.60		
Total	596	78.20		
Ln length				
Treatment	1	0.004	0.27	0.60
Month	5	0.08	1	0.42
Treatment×Month	5	0.23	2.87	0.014
Residual	587	9.35		
Total	598	9.66		

Litter size 2000-2001
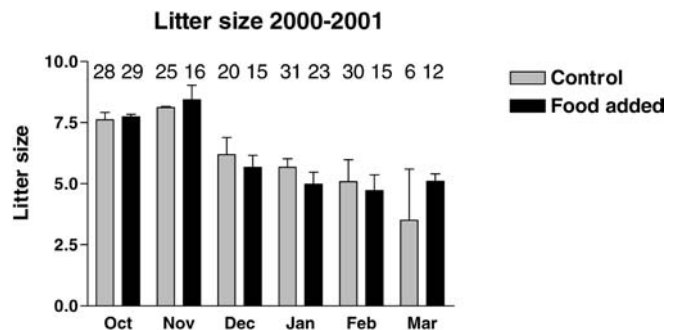
Fig. 3 Number of embryos (litter size) of breeding females obtained from necropsies. The *bars* represent averages of two farms for both food addition treatment sites and controls. *Numbers above the bars* show the numbers of breeding females. *Error bars* are SD. For other abbreviations, see Fig. 1

There was no significant variation in body length between months.

Reproduction and the length of breeding season

The litter size of breeding females was highest in November – in controls (8.1±2.1) and treatments (8.4±1.2) and decreased to 4.5–5.0 in March (repeated measures ANOVA, Wilks' λ=18.2, P=0.001) (Fig. 3). There was no effect of food addition on litter size (between-subject effect F=0.101, P=0.757).

The proportion of breeding females was highest in November and decreased steadily until March (F=18.30, df=5, P=0.003) (Fig. 4). There was no difference in the monthly proportions of breeding females between treatments and controls (treatment F=1.90, P=0.226, treatment×month interaction F=0.428, P=0.821). In March 20% of females were breeding in food addition areas and 16% in controls. In June there were no breeding females at either site.
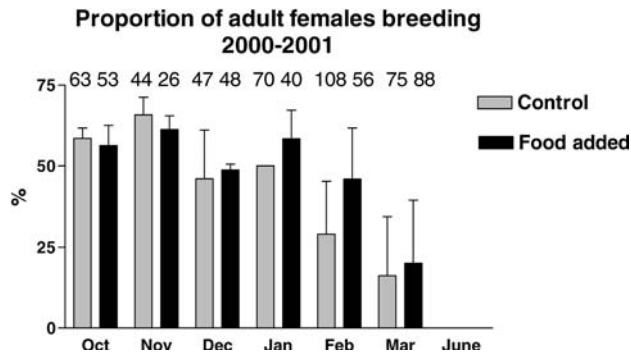
Fig. 4 Proportion of adult females breeding based on the total number of adult females (>72 mm). The total number of adult females in the sample is given *above the bars*. The bars represent averages of two farms for both treatments and controls. *Error bars* are SD. For other abbreviations, see Fig. 1

Discussion

Neither food quantity nor quality affected the breeding of house mice in our study. This was unexpected given the results of previous food additions in small mammal populations (review by Boutin 1990). However, we did not observe any changes in individual female reproductive performance (litter size, length of breeding season) or general reproductive patterns in the populations (extension of breeding, litter size dynamics). If food quality and quantity would have been, as we expected, a triggering mechanism for enhanced breeding in mice during an incipient plague, according to power analyses our data should have been able to show the effect between supplemental feed areas and controls.

Optimal food supply enhances the feeding abilities and reproductive success in birds (Martin 1987; Boutin 1990). Mammals differ from birds in parental care, and hence the reproductive trade-off might be different for them. Rodents, in particular, are supposed to be income breeders (Stearns 1992; Jönsson 1997); they do not collect any reserves for breeding or surviving but allocate improved food supply directly in reproduction. Therefore, especially in mice and voles, we would expect relatively strong effects of resources enhanced by food supplementation. During the mature standing crop and for about 2 months after harvest background food quantity and quality were high and the mice were not food constrained. Through chance, the amount of spilled grain was somewhat higher and the quality of grain was significantly higher on our food-supplemented areas further enhancing the food resources. Thus our treatment should have offered excellent food availability throughout the study. However, this did not result in an enhancement of parameters of female reproduction.

All reproductive parameters measured resembled those during an average non-plague year (Singleton et al. 2001), yet the population densities were the fifth highest recorded for June in 20 years in the study area. Despite the relatively high densities in spring and an early start of breeding (Pech et al. 2001) there was an early cessation of breeding in February–March, which dampened the amplitude of the population in June.

Rainfall is one of the main factors used in the forecast models of house mouse plagues in southern Australia (Brown and Singleton 1999; Pech et al 1999). A sufficient amount, and the timing, of rain can influence food supply and access to burrows (Newsome 1969). However, our study sites had sandy loam soils where mouse burrowing seemed not to be a problem.

Access to food for the duration of the study also was not limiting, especially on the food supplementation sites, although there appeared also to be an adequate quantity of food on the control sites. This then turns the focus to food quality. Why did female mice on the treatment site cease breeding in February–March at the same time as the control sites? There are two possibilities. One is that the high protein levels of the supplemented food may have required higher water turnover rates to metabolise this food. If so then this would require access by mice to free-standing water, which was not available during the hot and arid months of January and February. House mice are generally regarded as being well adapted to aridity (Fertig and Edmonds 1969). However, it is possible that female mice are not able to increase their energy intake two–threefold (as is the case for bank voles *Clethrionomys glareolus*, Kaczmarski 1966) to maintain breeding on a high-protein diet during dry and hot summer when water is lacking. We suggest therefore that there is a metabolic barrier for mice to turn the existing food resources into increased reproduction due to the lack of water. This conclusion is consistent with water turnover studies on mice in Australian grain fields (Mutze et al. 1991) and in California (Newsome et al. 1976) that summer aridity may suppress population size, breeding and survival of house mice.

Bomford and Redhead (1987) increased food protein from 8% to 11% in a field experiment with Australian house mice. They observed a significant increase in the proportion of females breeding but not in litter size. In our study the protein content of grain in the food addition areas was always >10% and our supplemental food had a higher protein content than that in Bomford and Redhead's study. However, we did not observe any improvement in either the proportion of breeding females or litter size. There are crucial differences between these two studies: our study was conducted earlier and during the main breeding season and in an arid area. The rice field habitat in the study by Bomford and Redhead (1987) and the high rainfall during their study may have provided the mice with access to standing water in the late breeding season in addition to the supplementary food. Further, the relatively small food-supplemented patches in their study might have predominantly attracted high quality females, which could have been reflected in the ability to continue breeding towards the winter.

In conclusion, rainfall might be an essential factor affecting reproductive changes but in a different manner than that suggested by Newsome (1969), Redhead et al. (1985) and Brown and Singleton (1999). The lack of

water might hinder mice to exploit the available high quality (but dry) food resources. It therefore appears that suitable conditions for reproductive changes in mice which will trigger a mouse plague form a complicated net of several factors, including good winter and spring rainfall (Pech et al. 1999) and occasional summer storms to dampen the effect of aridity on breeding performance.

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