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Is the reproductive potential of wild house mice regulated by extrinsic or intrinsic factors?

J. JACOB,[1,2]* L. A. HINDS,[1,2] G. R. SINGLETON,[1,2] D. R. SUTHERLAND[2,3] AND H. YLÖNEN[4]

[1]*CSIRO Sustainable Ecosystems, Canberra, ACT,* [2]*Pest Animal Control Cooperative Research Centre, Canberra, ACT,* [3]*School of Biological Sciences, Monash University, Clayton, Victoria, Australia; and* [4]*Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland*

Abstract The regulation of reproductive performance in small mammals may be determined by extrinsic or intrinsic parameters. In a large-scale, replicated field experiment we monitored the seasonal fluctuation in food availability and tested the effects of food addition on the reproductive performance of wild house mice (*Mus domesticus*) in south-eastern Australia. Ovulation rates and litter size increased during spring and peaked in October/November. Ovulation rate was consistently higher than litter size by approximately 1.2 embryos (19%). None of the extrinsic parameters measured (food quality and quantity, mouse abundance) had an impact on reproductive performance. The addition of food did not prevent the mid summer decrease in ovulation rates nor did it alter the difference between ovulation rates and litter size. While the number of previous pregnancies did not affect reproductive performance, the age of mice did: older mice tended to have higher ovulation rates than younger mice. The effect of age-dependent changes in ovulation rates on population growth rates of house mice seemed to be of limited importance. We conclude that the reproductive output in wild house mice is determined by ovulation rates and not by litter size. The regulation of ovulation rates through an intrinsic factor (age) seems evident but the importance of food availability and house mouse abundance for ovulation rates is low.

Key words: age, food supplementation, *Mus domesticus*, parity, reproduction.

INTRODUCTION

Among birds and mammals, food is a key factor that can limit reproductive performance (e.g. Boutin 1990; Doonan & Slade 1995; Wauters & Lens 1995; Predavec 2000). Variation in litter size can occur as a function of food resources, season, age and parity (see Sikes & Ylönen 1998 for a review).

Reproductive performance in small mammals is usually measured by the number of embryos produced or the number of pups born (e.g. Bronson 1979; Morris 1992; Veloso & Bonzinovic 2000; Singleton *et al.* 2001). Seasonal, annual or multiannual changes in these reproductive measures are then used to explain changes in abundance or demography of animal populations. However, there may be considerable seasonal fluctuations between the number of embryos conceived and the number of eggs shed. The mechanisms that influence changes in ovulation rates are often not clear in field populations. Favourable food resources could be one such mechanism that leads to high ovulation rates, as suggested for field populations of the red fox, *Vulpes vulpes* (Lindstrom 1988) and lynx, *Lynx lynx* (Brand & Keith 1979).

In south-eastern Australia, wild house mice, *Mus domesticus*, live in grain-growing regions. There, the seasonal supply of food from winter cereals that extend from October to February is thought to affect reproductive performance in house mice (Kenney *et al.* 2003). In addition, reproductive performance may be influenced by stochastic changes in the availability of high quality food (Kenney *et al.* 2003) possibly through germinating grass seeds after unusual summer rain as suggested by White (2002). Wild house mice undergo sporadic outbreaks in the grain-growing regions of south-eastern Australia where they then cause considerable damage to crops (Redhead & Singleton 1988; Singleton & Redhead 1990). These fluctuations are less regular than those of other small mammal species including voles and lemmings (Korpimäki *et al.* 2004).

*Corresponding author. Present address: Federal Biological Research Centre for Agriculture and Forestry, Institute for Nematology and Vertebrate Research, Toppheideweg 88, Münster 48161, Germany (Email: j.jacob@bba.de).

Present address: L. A. Hinds, CSIRO Entomology, Black Mountain Laboratories, Clunies Ross Street, Black Mountain, ACT 2601, Australia; G. R. Singleton, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines; D. R. Sutherland, Department of Environment and Conservation, Dwellingup Research Centre, Banksiadale Road, Dwellingup, Western Australia 6213, Australia.

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In Australian grain fields, house mice generally begin breeding in spring with a litter size around six, have a maximum litter size in early summer of about nine when the standing grain is ripening, and a steady decrease in litter size in late summer and autumn (mean litter sizes as low as four) (Singleton *et al.* 2001). Prenatal mortality is negligible and the timing of the annual fluctuation in litter size does not vary much between years (Singleton *et al.* 2001). Manipulations of food available to mice in the field had no effect on embryo numbers (Ylönen *et al.* 2003) and contrasting effects on the proportion of breeding females (Bomford & Redhead 1987; Ylönen *et al.* 2003). There is no published information on the effects of maternal age on reproductive performance in wild house mice or on the relationship of ovulation rates and litter size under fluctuating food availability.

During and after the breeding season in 2000/01, we monitored reproductive performance, maternal breeding history and age in wild house mouse populations in the grain-growing region of south-eastern Australia. Furthermore, we manipulated the food supply for house mice by providing high quality food pellets in the field at a time when breeding usually ceases. This simulated continuing stable food condition during the time when resources become scarce towards autumn. We aimed to explore the relationship of food supply, ovulation rates and intrauterine litter size and predicted: (i) that ovulation rates of mice would track the seasonal change in food quantity (grain crops, weeds) and food quality (grain crops); (ii) that maternal age would positively affect the reproductive performance of female house mice throughout the breeding season; and (iii) that the provision of supplemental food together with increasing parity would increase ovulation rates towards the end of the breeding season.

MATERIALS AND METHODS

We conducted this study at Walpeup (35°08′S, 142°02′E) in the Victorian Mallee of south-eastern Australia. We caught mice in four grain and sheep farms, with alternating paddocks of crop, fallow and pasture each of about 200 ha. Crops were winter cereals (mainly wheat intercropped with barley). Along fence lines between the paddocks was a stretch of 3–7 m of uncropped land.

Background food availability

From December 2000 to March 2001 we estimated food quantity monthly using quadrat sampling of spilled grain in one paddock per farm. In each paddock, topsoil to the depth of 2–3 cm was collected from 30 quadrats each 0.1 m^2. We estimated food quality based on the protein content of grain at three locations per month per farm. In November, during the standing crop, we sampled 50 heads of grain from one paddock in each location. Two heads were taken inside the crop, 25 m from the fence, at 25 sites 10 m apart along a transect of 240 m. Post harvest, the grain from the quadrat sampling was analysed for protein content. The grain was dried at 50°C for 24 h, seeds separated, milled and crude protein content as %N was detected using the Dumas technique (see Jacob *et al.* 2003 for details). The mean of these measurements was calculated per parameter, month and farm and used as an indication of food quantity and quality across a farm.

Food manipulation

From November 2000 until the end of the study in March 2001, high protein pellets (18–20% protein content) were provided ad libitum on two farms. We spread about 2 kg of pellets per fence line each week in November and 4 kg per week after that. Using a commercial bait spreader, we spread pellets 1–2 m within the uncropped area between the fence and the crop, and up to 12 m into the crop adjacent to the fence. For details see (Ylönen *et al.* 2003). During the breeding period, house mice are stationary (Krebs *et al.* 1995) and residents were assumed to have access to the food pellets. About 80% of female house mice trapped within the treated area ate the pellets (Jacob *et al.* 2003) and weekly visual estimates verified that pellets were available at all times.

Trapping

Mice were trapped monthly along fence lines and in the adjacent crop ($n = 2$) on each farm from October 2000 to March 2001 and on one farm only in September 2000. The distance between farms was 5–8 km and between fence lines >400 m. We placed one line of 10–24 Longworth live-traps along each of the fence lines and a second line of 10–24 traps in the adjacent crop with a spacing of 10 m between traps. The distance between traplines was 10 m. The fence lines were located between crop-crop or crop–pasture interfaces and each fence line was used only once for removal trappings. Traps were baited with wheat in the evening and checked shortly after sunrise for 6–7 consecutive days. Capture-mark-release was conducted for the first three nights. All mice captured after that were transferred to the laboratory, killed by cervical dislocation and females autopsied to estimate their reproductive performance and breeding history.

Age of these mice was estimated based on regressions of eye lens weight on known age (Sutherland *et al.* 2004). Known-age mice were derived from mice

caught in our study area in 2001. Mice were grouped in 2-month age-classes. Along additional untreated fence lines (one per farm) mice were trapped monthly for estimation of mouse abundance without kill sampling. Adjusted trap success (ATS) (Caughley 1977) for this fence line and for the two fence lines where mice were trapped and autopsied, was calculated and the mean used as a measure of mouse abundance across a farm. During the 2000/01 breeding season trap success was a good measure of mouse abundance because capture probability was largely constant (Jacob *et al*. 2004).

Estimation of reproductive performance

The number of ovulations, embryos and numbers and sets of uterine scars were counted to assess reproductive performance and breeding history of females. To assess ovulation rates, ovaries were collected at the time of autopsy and fixed in Bouin's fixative for 24–48 h before being transferred to 70% ethanol. Ovaries were then trimmed to remove the surrounding tissue before dehydration through to 100% ethanol before embedding in wax. Sections (6 μm) were prepared – the initial three sections were mounted, then 40 μm of tissue was discarded. This procedure was repeated until the full ovary was sectioned. Corpora lutea were about 100 μm wide and this method should have resulted in the detection of all corpora lutea present. The sections were stained with haematoxylin and eosin and the presence and stage of luteal structures in both ovaries of each animal was assessed using a light microscope (×40 magnification).

Three types of structures could be identified: new ovulations (new corpora lutea), recent corpora lutea of pregnancy and corpora albicantia (previous cycles). In most instances only two types of luteal tissue were present (new and recent corpora lutea). Each section was drawn and luteal structures identified and assigned to one of the three categories. Once all sections had been assessed, the total number of each type of luteal structure was determined. The gestation period of house mice is about 19 days (Parkes 1926). For all three ovulation categories, the number of embryos and the number of recent uterine scars, we calculated the week of conception based on the trimester of pregnancy (first trimester, embryos <1.6 mm; second trimester, embryos 1.6 mm to 10.5 mm; third trimester, embryos >10.5 mm) (Rugh 1990). Ovulation rates relating to the current pregnancy, as well as numbers of embryos, were backdated 1 week per trimester. If we found recent uterine scars in non-pregnant mice, ovulation rates relating to that pregnancy were backdated 4 weeks. Recent scars in pregnant females were backdated 4 weeks plus 1 week per trimester of the recent pregnancy. For new ovulations we assumed conception in the week of capture. Then, data for ovulation rates, numbers of embryos and numbers of recent uterine scars were grouped in 3-week intervals for all mice starting from the second week of August. A subset of the data on embryo numbers reported by Ylönen *et al*. (2003) were incorporated in our dataset backdated to the time of conception and supplemented by counts of uterine scars to assess the effects of food supplementation on the relationship of embryo numbers and ovulation rates. The number of sets of uterine scars was used as an indication for the number of previous pregnancies. Data were combined for the two fencelines sampled per month and farm.

Population growth rate

We simulated population growth rates (r) for September 2000–March 2001 for populations containing 25%, 50% or 75% of mice ≥5 months old (remainder of the population <5 months old). Simulations were based on observed data for trap success and ovulation rates of mice (<5 months old and ≥5 months old) for the early and late breeding season. Changes in ovulation rates were directly translated into changes in r.

Statistical analyses

General linear regression models were used to compare seasonal change in ovulation rates, litter size and the difference between ovulation rates and litter size among farms, with and without food addition and among 3-week intervals (ln-transformed data). The same method was used to explore the impact of environmental parameters on reproductive performance. The effects of protein content of grain, the amount of spilled grain and ATS on reproductive performance were tested simultaneously (farm + 3-week interval + protein content of grain + spilled grain + ATS) and separately. We also tested the effect of spilled grain and ATS on reproductive performance (6 weeks forward from current 3-week period of conception because the peak of reproductive performance and the peak of food availability were about 6 weeks apart) with identical regression models. The effect of age (2-month classes) and individual breeding history on reproductive performance was assessed for the early (October–December) and late (January–March) breeding season using general linear regression models (age: farm + age + age^2 + season + season · age + season · age^2; number of previous pregnancies: farm + number of previous pregnancies + season + farm. number of previous pregnancies + season. number of previous pregnancies). Data were ln-transformed if required to achieve normal distribution and/or equal variance. All tests were run in Genstat 6th edition (Genstat, Rothamsted

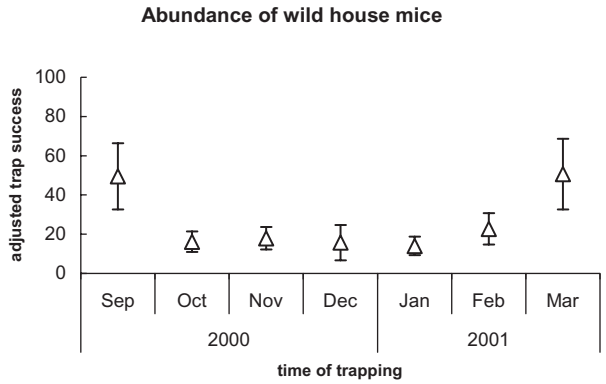

Fig. 1. Mouse abundance (adjusted trap success) for wild house mice from four grain farms in south-eastern Australia during the breeding season 2000/01. Error bars are ±1 standard error.

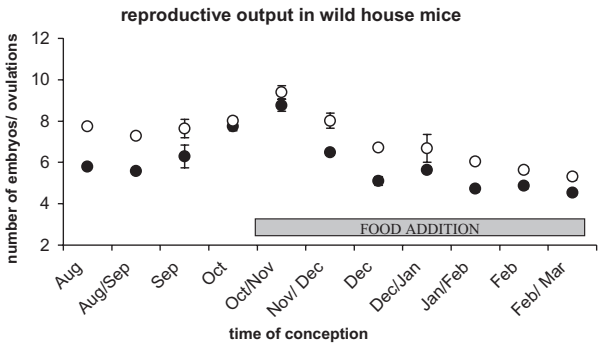

Fig. 2. Ovulation rates (number of corpora lutea or corpora albicantia – open circles) and intrauterine litter size (number of embryos or recent placental scars – black circles) in mice from four farms in south-eastern Australia during the breeding season 2000/01. Error bars are ±1 standard error.

International, Harpenden, UK). Uncertainty is stated as standard error throughout the paper.

RESULTS

We trapped 124 ± 17 mice per farm per month for estimation of mouse abundance. Information about female reproduction was obtained from 463 individuals providing ovulation rates (mean sample size per month and farm = 16), litter size (mean sample size per month and farm = 13) and the difference between ovulation rates and the number of embryos (mean sample size per month and farm = 12). Mouse abundance (ATS) differed among farms ($F_{3,588} = 694.9$, $P < 0.001$) and month of trapping ($F_{6,588} = 202.9$, $P < 0.001$) (Fig. 1).

Reproduction of house mice

There was no difference in ovulation rates of mice between farms with (mean 6.3 ± 0.2) and without food addition (6.2 ± 0.2) ($F_{1,17} = 0.01$, $P = 0.921$). Similarly, there was no difference in litter size (food addition: 5.2 ± 0.2; no food addition: 5.3 ± 0.2; $F_{1,17} = 0.02$, $P = 0.894$) and in the difference between ovulation rates and litter size (food addition: 1.36 ± 0.1; no food addition: 1.26 ± 0.1; $F_{1,17} = 3.47$, $P = 0.08$) between farms with and without food addition. There was no significant interaction between the factors food addition and 3-week interval in explaining litter size, ovulation rates and the difference between litter size and ovulation rates.

There was a constant difference between ovulation rates and litter size between farms ($F_{3,412} = 1.09$, $P = 0.352$). Although there was a suggestion of a reduced difference between ovulation rates and litter size in October and November, it was constant (1.2 shed eggs, which is a loss of 19% after ovulation) among 3-week intervals ($F_{10,412} = 1.55$, $P = 0.119$) (Fig. 2). Therefore, and because sample size was larger for ovulation rates than for litter size, further analyses were restricted to ovulation rates. The effect of 3-week intervals ($F_{10,606} = 15.70$, $P < 0.001$) on ovulation rates (Fig. 2) was higher than the farm effect ($F_{3,606} = 3.48$, $P = 0.016$). Ovulation rates increased from August (8.0 ± 1.1) to their peak in October/November (9.4 ± 0.3). After that ovulation rates dropped to ≤6 in January/February (Fig. 2).

Background food availability and mouse abundance

The amount of grain left in the fields differed among the months of trapping ($F_{3,9} = 15.09$, $P < 0.001$) with a considerable decrease from after harvest in December 2000 (206 ± 31 kg ha^{-1}) to March 2001 (36 ± 10 kg ha^{-1}) (Fig. 3). Assuming only mice fed on spilled grain and consumed about 3 g day^{-1} (Newsome 1967) about 395–2300 mice ha^{-1} could have been sustained by spilled grain per month from December–March (Fig. 3). The protein content of grain was 9.6–10.6% and differed among months of trapping ($F_{4,37} = 3.58$, $P < 0.001$) with high values >10% in November, February and March.

There was no effect of the protein content of grain or the amount of spilled grain left post harvest on ovulations ($P > 0.206$). The same was true for ATS and for these parameters 6 weeks forward from the current 3-week interval ($P > 0.134$).

Effects of season and individual parameters

Ovulation rates were 1.8 ovulations higher in the early than late breeding season ($F_{1,443} = 59.42$, $P < 0.001$)

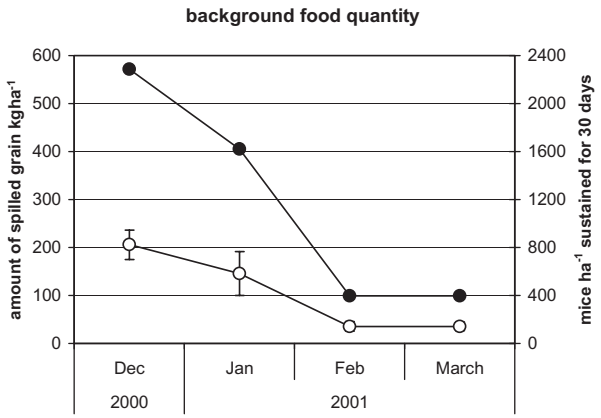

Fig. 3. Background food quantity (spilled grain after harvest – open circles) and the number of house mice sustained by spilled grain per month (assuming 3 g day^{-1} grain consumption per mouse – black circles) for mice from four grain farms in south-eastern Australia during the breeding season 2000/01. Error bars are ±1 standard error.

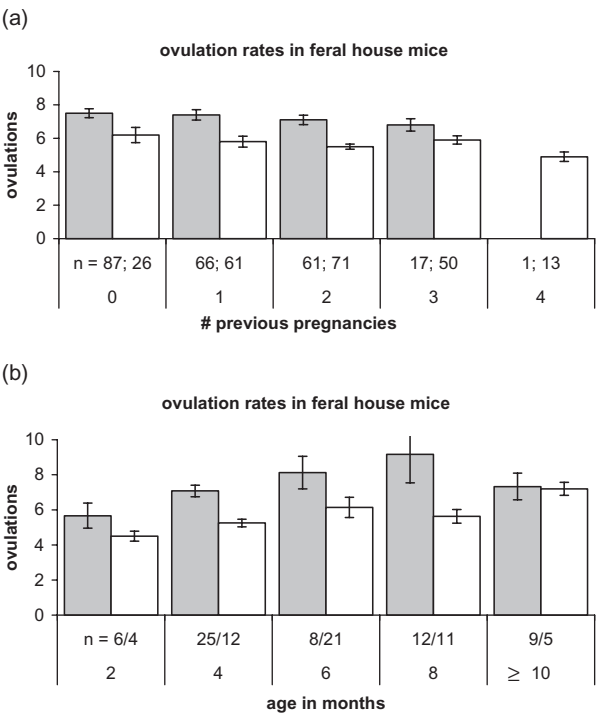

Fig. 4. The impact of (a) the number of previous pregnancies and (b) the age in 2-month classes on ovulation rates of wild house mice in early (October–January, grey columns) and late breeding season (January–March, open columns). Mice were from four farms in south-eastern Australia during the breeding season 2000/01. Error bars are ±1 standard error.

(Fig. 4a). There was a continuous but statistically not significant decrease in ovulation rate with increasing numbers of previous pregnancies in the early breeding season of about 0.7 shed eggs and an almost continuous decrease in the late breeding season of about 1.3 shed eggs ($F_{1,443} = 1.95$, $P = 0.163$). None of the interactions tested was significant.

Ovulation rates were higher for older mice than for young mice ($F_{1,105} = 6.33$, $P = 0.013$), and higher in the early than in the late breeding season ($F_{1.105} = 9.44$, $P = 0.003$) (Fig. 4b). There was an almost continuous increase of ovulation rates with age in the early and late breeding season with the minimum of 4.5 ± 0.3 for mice ≤2 months in the late breeding season and the maximum of 9.2 ± 1.6 for 7- to 8-month-old mice in the early breeding season. None of the interactions tested was significant.

DISCUSSION

At the moderate densities in our study, ovulation rate and litter size varied seasonally but there was no obvious impact of extrinsic factors. Contrary to our first and third prediction the ovulation rate was neither related to the present nor future background food quality and quantity. We were able to verify our second prediction, that maternal age positively influences ovulation rates throughout the breeding season.

Studies in boreal rodents have demonstrated a positive correlation between maternal age and the number of offspring produced per pregnancy (Myers & Master 1983; Nakata 1984). In feral house mice this has not been demonstrated previously. Age is correlated with body size to a certain degree, so the causal factor for larger litters at older age remains unclear (Stenseth & Gustafsson 1985). The correlation should become weaker when the increase in body weight decelerates for older mice (Redhead 1982). The increase in ovulation rates with increasing age for mice older than 4 months in our study suggests that age affects ovulation rates and consequently litter size. Larger mice have higher litter sizes and more large and possibly old mice breed during plague years compared with years of low mouse abundance (Singleton *et al.* 2001). Therefore, the higher reproductive performance of older mice may play an important role in plague years. Although ovulation rates were lower in the late breeding season than in the early breeding season for both young and old mice, a difference of at least 1.5 shed eggs was maintained between 2-month and 5- to 9-month-old mice. This equals approximately 20% of pups produced per litter in the late breeding season and is similar to values in ricefield rats (*Rattus argeniventer*) where 5- to 12-month-old females produce about 30% higher litter size than 1- to 2-month-old rats (Rahmini *et al.* 2003).

Model simulations indicated that the increased contribution of older females to population growth was about 12% of *r* and differences to observed values were most evident in the late breeding season (Fig. 5).

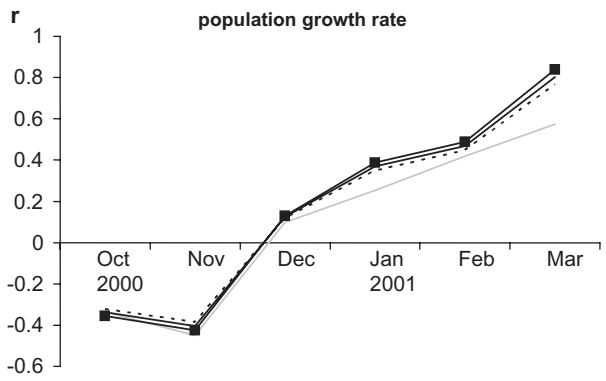

Fig. 5. Monthly population growth rate for house mice in grain fields based on trap success. Observed data (grey line) are compared with simulations of population growth for populations with 25% (broken line), 50% (solid line) or 75% (black squares) mice ≥5 months old.

Median age of house mice increased during the late breeding season from 4 to 5.5 months (Sutherland *et al.* 2004), which should have led to increased mean ovulation rates. However, ovulation rates decreased during the late breeding season suggesting that other factors than ovulation rates and food availability (see below) determined population growth rates.

Prerequisites for an outbreak of house mouse populations seem to be an early onset of breeding and an extended breeding season, driven by April to October rainfall (Pech *et al.* 1999), but not all years with these characteristics produce a plague (Singleton *et al.* 2001). Several studies have shown that supplementary food can increase the reproductive performance in small mammals and birds (Boutin 1990). In south-east Australia, house mice can take advantage of favourable food conditions through extending their breeding season, which generally leads to an outbreak in the population density of mice (Singleton *et al.* 2001). Food availability through spilled grain reached its minimum by February/March 2001 when mouse abundance was high. Even if we assume that all spilled grain was accessible for feeding and all mice present were trapped, at this time mouse abundance in some populations came close to or exceeded the number of animals that could have sustained by spilled grain (ca 395 mice ha^{-1}) by up to 40%. Therefore, we expected an additive effect of increasing female age and food supplementation in a way that food supplemented females would have been able to maintain higher ovulation rates despite a decline in natural food resources in the late breeding season. Even though embryo numbers were not directly affected by the food supplementation (Ylönen *et al.* 2003), we expected ovulation rates to respond directly or with a time lag to improved food availability.

However, mouse populations on our study site did not show an increase in the proportion of breeding females or the length of the breeding season where food was added (Ylönen *et al.* 2003). This was in contrast to food additions for mice in irrigated rice fields (Bomford & Redhead 1987). Ylönen *et al.* (2003) concluded that a lack of water in arid south-east Australia might not allow mice to metabolize and translate high quality food into reproductive performance. This may also be the case for ovulation rates.

Australia's grain-growing regions create a temporally and spatially synchronous pulse of high quality food supplied by the maturing grain crop in almost every year since cropping began about 100 years ago. This is equivalent to about 300 generations of mice, which may be sufficient for mice to adapt to seasonally available food supply. Seasonal variation in litter size in house mice has been reported in populations living in corn ricks in the UK (Berry 1981) and in grass sedges on a subantarctic island (Matthewson *et al.* 1994). There, house mice may experience a seasonal fluctuation of litter size depending on the availability of food as a mechanism of optimal resource allocation.

The Australian house mouse system does not seem to fit into the seasonality hypothesis (Ricklefs 1980), which considers regularly fluctuating resource availability to play a dominant role in determining litter size. Similar dynamics have been reported for bank voles, *Clethrionomys glareolus* (Döhle *et al.* 1991). Although the reproductive performance of house mice in our study appeared to track closely a seasonal change we could not find an extrinsic factor responsible for this. The presence of ripening and maturing grain seeds may be vital for triggering and maintaining breeding in Australian house mice (White 2002). This may be done through the occurrence of high levels of soluble amino acids in ripening seeds (White 2002) which may not only provide energy required for reproduction but directly or indirectly signal to the brain whether caloric levels are sufficient to engage in reproduction. This may be the case for leptin in baboons, *Papio anubis* (Banks 2003). If ovulation rates intrinsically regulate resource allocation for reproduction in mice this is probably not simply related to the food provided by grain crops. Food from other sources such as grasses, dicotyledons and arthropods also are eaten by mice in grain fields (Tann *et al.* 1991), but their availability was not measured in our study.

In conclusion, the reproductive output in wild house in Australian grain fields is mainly determined by ovulation rates. Our study showed that ovulation rates are regulated through an intrinsic factor (age) but this regulation may be of limited importance for the population growth rate of house mice in Australian grain fields. The relevance of food availability and mouse abundance for reproductive output of house mice is low but these parameters are likely to affect the fate of litters produced, which is crucial for population growth. No matter what the underlying cause for

fluctuations in ovulation rate is, an adjustment of ovulation rates to environmental conditions is probably more efficient than having constantly high ovulation rates with an adjustment of intrauterine litter size. Field experiments manipulating the availability of water and other environmental factors are needed to clarify whether the ovulation rates of house mice can be increased or maintained at a high level in late summer and autumn.

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