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Can outbreaks of house mice in south-eastern Australia be predicted by weather models?

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Abstract. Outbreaks of house mice (*Mus domesticus*) occur irregularly in the wheat-growing areas of south-eastern Australia, and are thought to be driven by weather variability, particularly rainfall. If rainfall drives grass and seed production, and vegetation production drives mouse dynamics, we should achieve better predictability of mouse outbreaks by the use of plant-production data. On a broader scale, if climatic variability is affected by El Niño–Southern Oscillation (ENSO) events, large-scale weather variables might be associated with mouse outbreaks. We could not find any association of mouse outbreaks over the last century with any ENSO measurements or other large-scale weather variables, indicating that the causal change linking mouse numbers with weather variation is more complex than is commonly assumed. For the 1960–2002 period we were only partly successful in using variation in cereal production to predict outbreaks of mice in nine areas of Victoria and South Australia, and we got better predictability of outbreaks from rainfall data alone. We achieved 70% correct predictions for a qualitative model using rainfall and 58% for a quantitative model using rainfall and spring mouse numbers. Without the detailed specific mechanisms underlying mouse population dynamics, we may not be able to improve on these simple models that link rainfall to mouse outbreaks.

Introduction

Since 1900 house mouse outbreaks have been an undesirable sporadic event in the wheat-growing regions of south-eastern Australia (Singleton *et al*. 2004). Detailed studies of local populations have been carried out at different sites for more than 40 years, and these studies provide a wealth of demographic data for understanding the causes of these outbreaks (Newsome 1969*a*, 1969*b*; Redhead and Singleton 1988; Mutze 1989, 1991; Singleton 1989; Mutze *et al*. 1990; Singleton and Redhead 1990; Boonstra and Redhead 1994; Pech *et al*. 1999; Singleton *et al*. 2001). If one understands the mechanisms behind demographic changes, the next step could be to construct quantitative models to predict outbreaks. For the house mouse in south-eastern Australia detailed modelling was undertaken by Pech *et al*. (1999, 2001), concentrating on the data available from Walpeup in the central mallee of Victoria. The Pech Model has been quite successful in predicting changes in mouse numbers in the central mallee (Pech *et al*. 2001), and Kenney *et al*. (2003) tried to extend this modelling effort to a broader spatial scale in Victoria and South Australia.

Two approaches for modelling mouse outbreaks are either to use long-term qualitative data on when outbreaks occurred with the imprecision of using newspaper reports from each State as data, or to use quantitative data available for the last 20 years to estimate precise models with the constraint of a shorter period and smaller sample size. In this paper we explore these two kinds of models and, in particular, try to determine whether we can use large-scale climatic measures related to the El Niño–Southern Oscillation (Thresher 2002) to predict mouse outbreaks in south-eastern Australia (Boonstra and Redhead 1994).

Materials and Methods

Qualitative house mouse data were dichotomised as 0 = no outbreak (too few mice to be noticed by farmers), or 1 = outbreak (damage reported by farmers), based on newspaper reports gathered by Saunders and Giles (1977); Mutze (1989); Singleton and Redhead (1989) and Cantrill (1991), and during the last 20 years from direct reporting from farmers and state agricultural scientists (Singleton *et al*. 2004). There are far more qualitative data available than quantitative data, and these data cover southern Queensland, New South Wales, Victoria and South Australia from 1900 to 2002 (Singleton, unpublished data; Mutze, unpublished data).

Quantitative house mouse data were available from two main sites: Walpeup in the Victorian mallee (Singleton, unpublished data) from 1983 to 2002, and Roseworthy in South Australia from 1979 to 2001 (Mutze, unpublished data). In addition, quantitative data were available from four other sites in Victoria and South Australia from 1998 to 2002

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(Fig. 1). Longworth and Elliott live traps were set in crops (typically 6 × 6 grids, 10-m spacing) and along fence lines (10-m spacing). Mouse abundance was estimated by adjusted trap success (no. caught per 100 trap-nights), and the general methods are described more completely in Mutze (1991) and in Singleton *et al*. (2001).

We chose nine areas as sampling sites for our analysis (Fig. 1). Cereal yield data from the period 1960–2001 were obtained from the Australian Bureau of Statistics for the statistical local areas shown in Fig. 1. Monthly temperature and rainfall data for the same period were obtained from the Australian Bureau of Meteorology for sites in or near the areas shown in Fig. 1. In a few cases for which rainfall data were missing from one station we used data from a nearby station for that period. In general, monthly rainfall data are highly correlated for nearby sites. In addition to temperature and rainfall, we have computed two weather variables to add in the analysis – actual evapotranspiration and soil water deficit. Actual evapotranspiration (AET) is a complex function of temperature and rainfall in association with potential soil water storage. Soil water deficit measures the shortage of water in the soil, and is maximal under drought conditions. Monthly actual and potential evapotranspiration were calculated for all rainfall stations from temperature and rainfall data. We used the methods of Thornthwaite and Mather (1957) to estimate actual and potential evapotranspiration and soil water deficit for the areas shown in Fig. 1. These estimates agreed with the general maps published by Wang (2001).

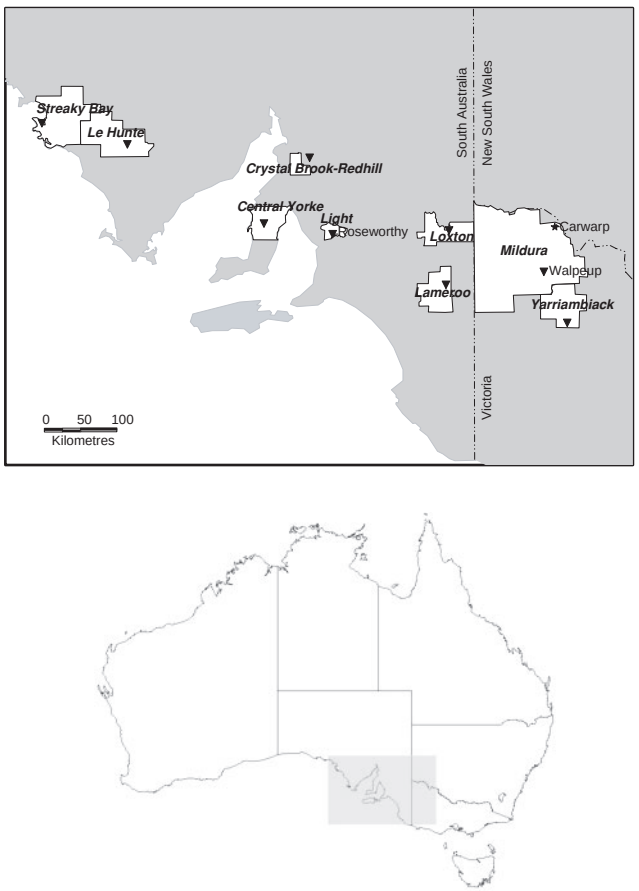

Fig. 1. Location of the study areas utilised in this analysis. The nine statistical local areas from which wheat production and qualitative mouse outbreak data were obtained are outlined. The meteorological sites from which rainfall and temperature data were obtained are indicated by a ▼ for each study area. The major long-term study sites of Roseworthy and Walpeup are shown. Quantitative data from 1998–2002 were also obtained from four other sites at Loxton, Lameroo, Yarriambiack (Beulah) and Carwarp. The natural vegetation of all these sites is mallee.

The current model for house mouse outbreaks is based on the assumption that food supplies cause changes in population density and that other intervening variables such as predation and disease produce only minor modifications in the patterns set by the food supply (Pech *et al*. 1999). Mutze *et al*. (1990) used wheat, barley and oats yield, and Pech *et al*. (1999) used wheat yield as a surrogate measure of food supply. In addition to wheat yield we obtained data on other cereal grains and hay production as surrogate measures of plant production. For large-scale weather variables, we obtained data on the Southern Oscillation Index from the Australian Bureau of Meteorology, National Climate Centre (http://www.bom.gov.au/climate/current/soihtm1.shtml) and information on the phase of the Southern Oscillation Index from Dr R. C. Stone (Stone *et al*. 1996 and personal communication). Additional large-scale data were obtained on sunspot numbers (http://sidc.oma.be/index.php3), the number of days per year with strong Zonal Western Winds, the mean latitude of the subtropical ridge, the Antarctic Circumpolar Wave (sea surface temperature at 50°S, south of Tasmania; see http://acw.ucsd.edu/ACW/) (Thresher 2002). These large-scale climatic variables are believed to be driven by the sunspot cycle and affect rainfall and temperature in south-eastern Australia. We used these large-scale weather variables as descriptors of ENSO events to explore whether they are useful predictors of mouse outbreaks.

For our first model, we have attempted the simplest statistical approach to predict whether or not there will be a mouse outbreak. We used biophysical data in logistic regression to estimate the probability of a mouse outbreak for each state for the 1900–2002 period (n = 408 state-years) using the large-scale regional climate measures.

For the second model we have attempted a more detailed prediction of how large the mouse population will be in the autumn, on the assumption that higher abundance in autumn translates into higher crop damage (Caughley *et al*. 1994). For sites and years for which we had quantitative data since 1979, we used robust multiple regression (Montgomery *et al.* 2001) to predict the maximum autumn mouse density for that year. The models developed by Pech *et al*. (1999, 2001) are based on predicting the rate of increase of mice, so that, if one knows the starting density of mice and some measure of food resources, one could predict the rate of increase and hence the abundance for the next time step (122 days in the 2001 model). We have adopted a different statistical approach here in trying to predict absolute density of mice in autumn from large-scale climatic measures.

In addition to using physical and biological variables to predict outbreaks and mouse abundance in the same biological year, we investigated whether the system was responding to time lags by using physical and biological measures of the previous 1–2 years to determine whether better predictability could be achieved.

All statistical analyses were carried out with NCSS 2001 (Number Cruncher Statistical System, Kaysville, Utah, www.ncss.com).

Results

We present our results as a series of questions with relevant data.

Can we predict mouse outbreaks from ENSO-type data?

The widespread nature of some of the mouse outbreaks in south-eastern Australia has led to the suggestion that they might be related to global climate shifts such as the El Niño–Southern Oscillation. For example, New South Wales, Victoria and South Australia had outbreaks in 1917, 1932, 1970, 1980 and 1984 (Saunders and Giles 1977; Mutze 1989;

Table 1. Pearson correlation coefficients (*r*) for the relationship of house mouse outbreaks in south-eastern Australia (0/1 scale) and the value of 5 large-scale climatic variables

Time series for some of the climatic variables do not extend back as far as the mouse outbreak data and this accounts for variable sample sizes (years). Mouse outbreaks were scored as 0/1 from newspaper and State Government reports and direct observations (see text for references). None of these correlations are statistically significant

State	Sunspot numbers	Antarctic Circumpolar Wave	Southern Oscillation Index	Days with strong Zonal Western Winds	Latitude of Subtropical Convergence
Queensland	0.09	0.37	0.10	–0.13	0.14
New South Wales	0.11	–0.02	–0.02	–0.05	0.07
Victoria	0.01	–0.10	–0.17	0.16	–0.01
South Australia	–0.04	–0.02	0.00	0.10	–0.12
Total all areas	0.06	0.10	–0.03	0.02	0.03
Sample size	103	17	103	55	93

Singleton and Redhead 1989). We could detect no significant logistic regressions for any of the 0/1 time series for the states when we utilised the independent climatic variables 'number of sunspots', 'the stage of the Antarctic Circumpolar Wave', 'the Southern Oscillation Index', 'the number of days with strong Zonal Western Winds' and 'the latitude of the Sub-Tropical Convergence' (Table 1). No single variable or combination of variables was significant statistically.

We investigated whether there might be a time lag in the response of house mouse populations to the weather conditions generated by these large-scale climatic disturbances by lagging the mouse outbreak score by one or two years. We failed to find any significant logistic regressions among the 20 tested (four states, five climatic variables) when we added a one-year or a two-year time lag, and again all the correlation coefficients were small and non-significant.

Because mouse outbreaks have apparently become more frequent since 1980, we divided the data and tested the 1900–80 data for these same correlations with large-scale climatic measures. There were no significant correlations between mouse outbreaks and large-scale climatic variables for these 1900–80 data either. Next we thought that perhaps the El Niño signature might be visible only at the very severe mouse outbreaks. We checked to see whether the major widespread outbreaks of 1917, 1922, 1932, 1970 and 1980 (ignoring all the less-widespread outbreaks) were associated with any of the large-scale variables, and again there were no significant correlations.

Because we had more specific quantitative data for mouse numbers from Walpeup and Roseworthy for the past 20 years, we also attempted to relate maximum autumn mouse numbers to these five large-scale climatic variables through the use of multiple regressions. Fig. 2 shows that mouse numbers at Walpeup and Roseworthy have fluctuated more or less in concert over the past 20 years. Prior to 1980 there were severe outbreaks in both areas in 1969–70 and again in 1979–80. In spite of this coherence between these two areas, which would suggest a general climatic driver, we were unable to find any significant relationships between the five large-scale climatic measures and autumn mouse abundance,

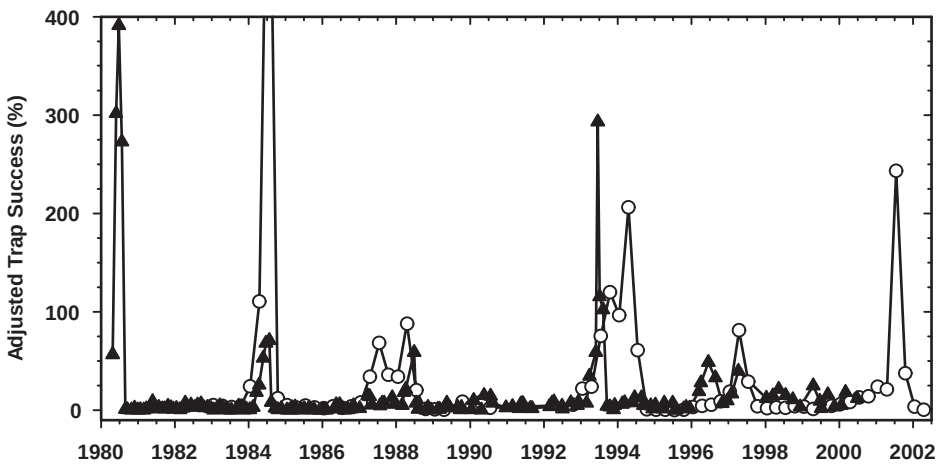

Fig. 2. Adjusted trap success for house mice in the Victorian mallee at Walpeup (open circles) and the South Australian mallee at Roseworthy (solid triangles). The correlation between these time series is 0.40 ($n = 58$). The 1979–80 outbreak at Roseworthy also occurred at Walpeup but we have no trap-success data for Walpeup until 1983. An outbreak also occurred at Roseworthy in 2001–02 but we have no quantitative measure of its size.

even at the 10% level. We also tried to estimate multiple regressions with a one-year time lag of mouse numbers, and again there were no significant variables.

We concluded that none of the large-scale ENSO-type climatic signals were useful predictors of a house mouse outbreak in south-eastern Australia. Similar conclusions were reached by Brown and Ernest (2002) for outbreaks of desert rodents in south-western United States.

Can we achieve a good prediction of grain supplies from available rainfall data?

If large-scale climatic variables cannot be used to predict mouse outbreaks, perhaps we can use more detailed measurements of plant production or local rainfall and temperature measurements as predictors. One reason why ENSO-type climatic signals cannot predict mouse outbreaks could be that rainfall and food supplies for mice are not closely related to these climatic drivers. If this is correct we may be able to achieve a better predictive model for mouse outbreaks by focusing directly on rainfall and temperature and their impact on food production. One of the two key variables in the Pech *et al*. (1999) model was wheat yield as predicted by autumn and winter rainfall. Wheat in this region is planted from late April to early June and harvested in November and December, 4–6 months before a mouse outbreak would reach maximum numbers. Previous analyses for the most part suggest that April–October rainfall can explain much of the variation in wheat yield from year to year (French and Schultz 1984). Seif and Pederson (1978) suggested that spring rainfall (September–October) was a better predictor of grain yield for wheat, and consequently we have explored all possible combinations of rainfall variables to see which ones might be best for our data.

We checked to determine whether yields of the cereal grains wheat, barley and oats were highly correlated with each other, and found high correlations (r = 0.90–0.93), with the same regression for all areas of the mallee shown in Fig. 1. For this reason we have concentrated all further analysis on wheat yield only as a surrogate for seed production. Wheat is the dominant crop in this region and should provide a good index of plant-growing conditions.

For the prediction of wheat yield from rainfall data, location (Fig. 1) does not matter, and all nine areas fit the same regression of yield on rainfall given in Fig. 3. The highest correlations for wheat yield and rainfall over all areas are with either May–October rainfall or April–October rainfall (r = 0.64, n = 302). No other rainfall grouping is superior to these.

If wheat yield is a good surrogate measure of food available to house mice, we need to determine the best set of variables for estimating wheat yields. Can we improve on the prediction of wheat yield by additional variables? Soil moisture levels are one possibility. Actual evapotranspiration (AET) in spring (from August to November) is correlated loosely with rainfall (r = 0.39–0.76) for the nine areas we have sampled, and consequently it might add some predictability to the above regression based on rainfall. No one seems to have used AET to predict grain yield. AET is closely related to soil moisture deficit (r = –0.88), and we have used soil moisture deficit to try to predict wheat yields.

We used multiple regression to obtain the best predictive model for wheat yield (t ha^{-1}) at the nine areas shown in Fig. 1 from 1960 to 2000 as follows:

$$\text{Wheat yield} = 1.38633 - 0.005456(\text{soil moisture deficit}) + 0.001472(\text{April–October rainfall}) \quad (1)$$

(r = 0.71, n = 279), where wheat yield is in tonnes per hectare, soil moisture deficit is in millimetres (summed for August–November) and rainfall is in millimetres. Essentially the same predictability could be achieved with AET rather than soil moisture deficit. We concluded that soil moisture or AET data add precision to the prediction of wheat yields over all areas, but that a substantial proportion (~50%) of the variance in wheat yields is not captured by any simple rainfall, soil moisture or AET measurements.

Can we use grain production figures to estimate the chances of a house mouse outbreak?

We used logistic regression to predict the probability of a mouse outbreak from observed wheat yield, using 256 annual observations over the nine sites shown in Fig. 1. The resulting logistic regression was:

$$\text{Logit(Y)} = 1.6226 - 1.1142(\text{Wheat yield}), \quad (2)$$

where wheat yield is observed yield in t ha^{-1} for the current biological year. For this regression, wheat yield ranged from 0.21 to 3.11 t ha^{-1}. The resulting logit can be converted to a probability by the equation:

$$\text{Prob(Outbreak)} = 1 / (1 + e^{\text{logit(Y)}}). \quad (3)$$

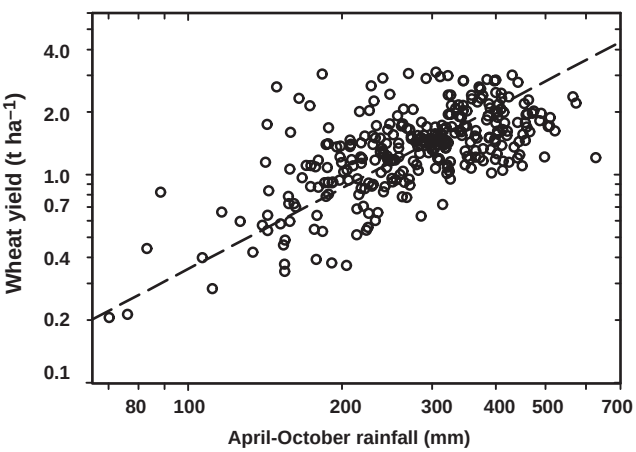

Fig. 3. Wheat yield as a function of winter rainfall from nine areas of Victoria and South Australia defined in Fig. 1, 1960–2001. n = 302, r = 0.64. The log–log functional regression line is: log (wheat yield) = –3.04029 + 1.29294log(April–October rainfall), where yield is in tonnes per hectare and rainfall is in millimetres.

The logistic regression model predicts the probability of an outbreak, and we have made the simplest assumption that when this probability is greater than 0.5, an outbreak is predicted. Classification of the 256 observations was correct 67% of the time when we used the conventional 0.5 probability threshold (Table 2*a*). If we set a lower threshold for action when the probability of an outbreak is greater than 0.3, we never miss predicting an outbreak when one actually occurs (Table 2*b*) but at the price of making the mistake of predicting an outbreak very frequently when one does not occur. For south-eastern Australia, for example, the cost of rodent control is approximately A$20 ha^{-1}, the possible losses ~A$100 ha^{-1}. With these economic costs the lower threshold model may result in a maximum economic benefit to a farmer (Davis *et al*. 2004).

We checked the finding of Mutze *et al*. (1990) that wheat yield both in the current year and in the previous year would affect mouse numbers, and found that nothing was gained by adding this variable into the logistic regression given above.

Are rainfall variables better than wheat yield for estimating the chances of a house mouse outbreak?

Using rainfall and soil moisture data, we explored many possible alternative predictive models for the probability of a mouse outbreak. The best model achieved by the use of physical parameters alone was (from Kenney *et al*. 2003):

$$\text{Logit(Y)} = 2.7325 - 0.0277(\text{November rain}) - 0.00780(\text{May–September rain}), \quad (4)$$

where rain is measured in millimetres. This logistic regression correctly classified 70% of the observations (n = 255), as reported in Kenney *et al*. (2003). Adding wheat yield to this rainfall regression improved predictability but by only 3% (73% of the 255 observations were correctly classified). Soil water deficit and AET were of no value in improving predictability. We conclude that the above logistic model based on rainfall, as reported by Kenney *et al*. (2003), is the most useful model at present for predicting qualitatively the chances of a mouse outbreak from physical parameters alone. This was unexpected since wheat yield is a key variable in the model of Pech *et al*. (2001) and is thus closer than rainfall measurements to the key food parameter that is believed to trigger mouse outbreaks.

Can we achieve a good quantitative prediction of mouse outbreaks from wheat yield?

We used the quantitative data from Walpeup and Roseworthy to determine whether wheat yield could be associated with maximum mouse densities in autumn. From the period 1980–2001 we used linear regressions to estimate this relationship. The Spearman rank correlation between maximum autumn trap success and wheat yield is 0.49, considerably higher than the Pearson correlation coefficient (0.21), suggesting a non-linear relationship. The log-transform of maximum abundance produced the best relationship, shown in Fig. 4. There is considerable scatter about this regression, suggesting that wheat yield provides only a poor predictor of autumn mouse densities (r = 0.40).

If we add rainfall variables to the regression of wheat yield on autumn mouse numbers we get a vastly improved model, with r = 0.70, and the contribution of wheat yield to the proportion of variance explained is only 5%. If we add to this model the September mouse abundance estimate, there is again a dramatic improvement in the predictive model, with r = 0.92. Wheat yield drops out of this model and the resulting multiple regression is given by:

$$\text{Maximum autumn abundance} = -23.4924 + 0.7469(\text{December rain}) + 0.10944(\text{April–October rain}) + 1.1490(\text{September trap success}), \quad (5)$$

with n = 43, all rain in millimetres, and September trap success measured as adjusted trap success. For this regression maximum autumn abundance ranged from 0.47 to 243, December rainfall ranged from 0 to 122 mm, April–October

Table 2. Classification table for the prediction of house mouse outbreaks in the Victorian and South Australian mallee regions from the logistic regression (Eqn 2) using wheat yield for 1960–2001 on the nine areas in Fig. 1

Boldface items indicate mistakes in classification. Two thresholds are illustrated: (a) the typical 50% probability threshold in which a mouse outbreak is predicted if the probability computed in the model is 50% or more, and (b) the lower 30% threshold. Outbreaks were classified qualitatively on the basis of moderate or severe damage to crops

		Estimated from model		Total
		No outbreak	Outbreak	
(a) Threshold probability for an outbreak 0.5:				
Actual event	No outbreak	142	**69**	211
	Outbreak	**15**	30	45
	Total	157	99	256
(b) Threshold probability for an outbreak 0.3:				
Actual event	No outbreak	35	**176**	211
	Outbreak	**0**	45	45
	Total	35	221	256

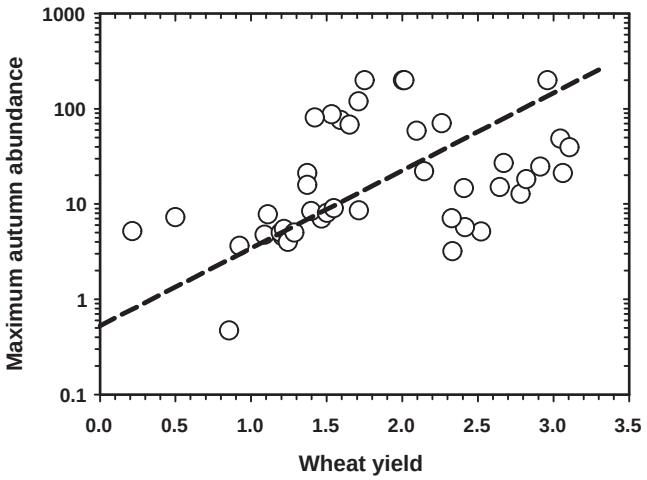

Fig. 4. Relationship of maximum autumn mouse numbers (log scale) to wheat yield for Walpeup and Roseworthy data, 1980–2000. Abundance is measured by adjusted trap success in autumn, wheat yield in tonnes per hectare in the same biological year. The functional regression [log(maximum autumn abundance) = –0.27946 + 0.81487(wheat yield) (n = 43, r = 0.40), variance about regression 0.3086] is highly significant.

rainfall ranged from 54 to 346 mm, and September trap success ranged from 0.22 to 146.

One consideration of these predictive models if they are to be applied is how early during the cropping season they can yield a prediction of mouse abundance in autumn. If we wish to have a 6-month warning of an impending outbreak, we will require a predictive model that is complete by October. The best of these minimal models is given by:

$$\text{Maximum autumn abundance} = -32.8624 + 0.2350(\text{April–October rain}) + 1.2680(\text{September trap success}), \quad (6)$$

which gives r = 0.82, a loss in predictability that is offset by an ability to provide earlier predictions for farmers.

The disappointing bottom line is that knowing wheat yield does not provide sufficient information to develop a good predictive model of house mouse outbreaks.

Discussion

A comparison of the predictions of the Pech Model with the current models for mouse outbreaks

The model described by Pech *et al*. (1999, 2001) has been applied very effectively at Walpeup in the Victorian Mallee, and can serve as a benchmark for comparison with the models described in this paper. To carry out this evaluation we utilised mouse data from four sites in the Mallee of South Australia and Victoria – Loxton, Lameroo, Carwarp and Yarriambiack (Fig. 1), all within a 100–200-km radius of Walpeup.

Table 3 summarises the results of these comparisons. In overall performance the model of Pech *et al*. (2001) is about equal to the complete Kenney model (Eqn 5) and better in performance than the minimal Kenney model (Eqn 6). All the models missed the minor outbreak at Walpeup in autumn 2001, although in November 2000 the Pech model predicted moderate mouse numbers in autumn 2001, which suggested the need for subsequent monitoring of mouse populations. This particular outbreak was an end-of-season spurt in mouse abundance, which rose from 53% in May 2001 to 243% in June 2001. All the other density estimates were at the low end of the scale at levels where crop damage is low and typically ignored. One disadvantage of the full Kenney model is that it requires December rainfall to complete its estimate for maximum autumn mouse abundance. Whether the minimal Kenney model (Eqn 6) can predict a full outbreak remains to be determined by future forecasts. The

Table 3. Comparison of the performance of the model of Pech *et al*. (2001) and the modified models of Kenney *et al*. (2003) presented in this paper for the prediction of maximal autumn house mouse numbers for five areas of the mallee regions of Victoria and South Australia, 2000 and 2001

Mouse numbers are given as adjusted trap success (%)

		Observed mouse abundance	Prediction from model of Pech *et al*. (2001)	Prediction from full model of Kenney *et al*. (Eqn 2)	Prediction from minimal model of Kenney *et al*. (Eqn 3)
Loxton	Autumn 2000	7.8	1.8	15.5	14.3
	Autumn 2001	1.2	1.1	27.7	12.1
Lameroo	Autumn 2000	75.9	19.6	77.0	35.5
	Autumn 2001	5.1	36.5	19.8	43.8
Carwarp	Autumn 2000	15.9	2.6	15.1	7.7
	Autumn 2001	7.0	5.8	25.0	33.7
Beulah	Autumn 2000	5.1	14.1	23.3	29.7
	Autumn 2001	6.5	37.5	22.6	33.7
Walpeup	Autumn 2000	12.8	0.1	40.3	19.8
	Autumn 2001	243.0	57.0	35.3	40.4
Sum of absolute deviations		–	347.0	336.0	392.7
Mean absolute deviation		–	34.7	33.6	39.3

results in Table 3 suggest that all of these three models are less accurate in their predictions than we would desire.

The full Kenney model is most sensitive to September trap success (standardised regression coefficient 0.67), less sensitive to December rain (0.43) and least sensitive to April–October rainfall (0.14). The coefficient of variation of these variables follows this order as well: 203%, 100% and 39% respectively. Given the existing range of data values for the three predictor variables, the model requires all of these to be ~2 standard deviations above the mean values to generate a hypothetical mouse outbreak.

Minor, local house mouse outbreaks, like those given in Table 3, could be partly driven by local immigration into favourable areas. We do not know the scale of dispersal movements of house mice in this region, but we presume it is on the scale of a few kilometres rather than tens of kilometres. We hypothesise that local outbreaks are caused more by local rainfall events, but we do not yet have rainfall data on a fine-enough spatial scale to test this idea.

Comparison of the present model to the mouse model of Mutze et al. *(1990)*

We compared the predictions of the model of Mutze *et al*. (1990) for house mouse outbreaks with those of the present model (Eqn 4). Mutze *et al*. (1990) used data for South Australia from 1900–84 to develop a logistic model (0 = no outbreak, 1 = outbreak) to predict the probability of an outbreak. We took their model (their Eqn 3) and applied it to the data we have analysed from 1960–2002. The model of Mutze *et al*. (1990) is of the form:

$$\text{Logit(Y)} = 5 + 3.5(\text{grain yield difference}) + 0.028(\text{November} - \text{October rain}) + 0.014(\text{autumn rain}),$$

where the grain yield difference was the grain yield this year minus the grain yield two years ago, the spring–early summer rainfall variable was November rainfall minus October rainfall, and the autumn rain was the total rain from March to May (in millimetres). From our dataset we had 200 site-years for which these data were available, and the model of Mutze *et al*. (1990) had a 19% error rate in prediction for these 200 data points. But these errors in the model of Mutze *et al*. (1990) were concentrated in the outbreak years, and 22 of the 40 outbreaks were not predicted correctly, a failure rate of 55%, compared with the equivalent failure rate of 32% for our model (Eqn 4 above, Kenney *et al*. 2003). Thus our current model has a higher predictive ability for outbreaks.

Nevertheless, the differences between our model and that of Mutze *et al*. (1990) are minor rather than major. In both models rainfall is critical, particularly in autumn and spring, and grain yields are also correlated with autumn mouse numbers.

Water balance may be a critical limitation to house mouse reproduction and survival in the summer (Mutze *et al*. 1991). We do not have the specific information needed to examine this idea from our crude measures of rainfall, but it may well be one important mechanism by which rainfall operates to influence mouse population trends.

Conclusions

We have explored two important questions in this paper. First, abundant evidence now exists of El Niño-type effects on the dynamics of terrestrial communities (Holmgren *et al*. 2001), and one might expect a widespread house mouse outbreak to map on some of these large-scale climatic indicators. We have explored this issue with qualitative data spanning the last 100 years and quantitative data from two areas spanning 20 years. In neither case can we detect any association of ENSO measures with mouse outbreaks, even if we allow for time lags. One problem with this analysis is that we have used political states as ecological units when clearly they are not uniform mouse habitats. We have tried to get around this problem by restricting analysis to only the major outbreaks that occurred in at least three of the four states in the same year, and even these major outbreaks could not be related to any ENSO-type measurements. ENSO variables are not well correlated with winter rainfall in the Mallee region, and it is these details of winter and spring rainfall that seem important to house mice (Saunders and Giles 1977).

Second, if rainfall drives plant production in the semi-arid Mallee regions of south-eastern Australia, we might expect to find that measures of plant productivity are better historical predictors of mouse outbreaks. We used observed wheat production as a surrogate for general grass production, and found only a modest association of wheat yield with mouse abundance (Fig. 4). When we introduced rainfall variables to the wheat yield regression, predictability improved greatly and overall wheat yield added very little to the final multiple regression model for predicting mouse abundance.

We can see two reasons why wheat yield has not emerged as a good predictor of mouse abundance. First, there may be no simple relationship between wheat production over the 1960–2001 period and measures of plant production that are relevant to mice. Simple relationships over this 40-year timespan are compounded by changing levels of fertiliser use, farming practices and grain varieties, especially over the period that we are analysing here (Hamblin and Kyneur 1993). Wheat may not be a good surrogate of plant production for winter grasses such as barley grass (*Hordeum vulgare*) that could be the key to early mouse reproduction (Bomford 1987; Singleton *et al*. 2001). Second, the simple model of mouse population dynamics given in Kenney *et al*. (2003) may be incomplete. If increased plant production is a necessary, but not sufficient, condition for triggering an outbreak of mice, we need to find the other factors that are necessary. These might involve changes in food quality (White 2002), predation pressure (Pech *et al*. 1999), disease

and parasites (Singleton *et al*. 1993), or changes in social organisation (Krebs *et al*. 1995). An alternative model would implicate the importance of invertebrate food in the mouse diet in late winter and spring (Tann *et al*. 1991), with the implication that invertebrate food abundance is not reflected in wheat production data. The importance of nitrogen in the diet, as emphasised by White (2002), could be an important component of this model. Brown and Singleton (1999) explored the rainfall model for house mouse outbreaks and pointed out that there is a biological memory lasting ~2 years in the mouse population that prevents sequential outbreaks from occurring. They suggested that one mechanism for this memory might be changes in age structure of the type discussed by Boonstra (1994).

Our conclusions are somewhat at variance with those of Mutze *et al*. (1990), who found that rainfall and wheat yield both were useful predictors of a mouse plague, but their rainfall variable included the difference between November and October rainfall, a term measuring the impact of too much rain at harvest time, and a wheat yield variable that was the difference between the wheat yield of the current year and that of two years before, a variable that could relate to soil nutrient storage. The model of Mutze *et al*. (1990) predicted outbreaks with an error rate of only 13% (27 of 31 years in which the model predicted >60% chance of a plague actually had an outbreak) for the South Australian data on which it was based. Unfortunately, the Mutze *et al*. (1990) model did not do as well when we applied it to our more extensive dataset from Victoria and South Australia from more recent years. Mutze *et al*. (1990) analysed data on wheat yields, rainfall and mouse outbreaks from 1901 to 1984. The difference between the present model and that of Mutze *et al*. (1990) may be more apparent than real, since both concentrate on rainfall and food supplies, and the central question is what exact variables to use to make effective predictions of mouse outbreaks. The timing of rainfall is as important as the amount of rain.

Do these results allow us to predict the regional mouse outbreak patterns observed in 1999–2002? The existence of small local outbreaks of mice, as found in recent years, for example, at Lameroo in autumn 2000 and Walpeup in autumn 2001, may become more common and if we have a good model we should be able to predict these local events. The sample size we have available so far is small and there is only a slight difference in the predictive precision of the models in Table 3. More data will be needed to make a rigorous comparison of these models. The model of Pech *et al*., like the minimal Kenney model (Eqn 6) needs only winter rainfall and spring mouse abundance to predict autumn mouse numbers, an advantage in early warning for farmers.

The earlier literature suggests much higher correlations between rainfall and wheat yield (r = ~0.8–0.9), suggesting that in more recent years these two variables are more independent. Clearly, we can wait until the data are in to determine wheat yield (January), but since our objective is to warn farmers of forthcoming mouse problems, we need to be able to predict at least 4–6 months in advance of a coming mouse plague (late October, early November). Hence the need to find some prior variables for predicting wheat yields.

Of the two models developed by Kenney *et al*. (2003) and further analysed here, we think the logistic model may be more useful to farmers who need to know in advance when to expect high mouse numbers in autumn. The quantitative model may be more useful for improving ecological understanding, and could become useful in practice if a simple way of estimating mouse abundance for September can be developed. The quantitative model and that of Pech *et al*. (2001) need to be compared with future data to determine which is better at quantitative predictions. None of these models reach the 90% level of accurate prediction we would like to achieve, although economic benefits can accrue even with less accuracy of prediction (Davis *et al*. 2004).

Future work

Future work should involve experiments to determine what factors set the start of the spring breeding season, which is highly variable in house mice. Insects and grass seeds are a major component of spring diet (Tann *et al*. 1991). The start of breeding could be examined with simple models that predict the onset of insect activity and grass seed production in response to preceding weather patterns. We suggest that more research on whether a barley grass growth model can predict the start of spring breeding in mice would be a useful addition to the present modelling effort. Detailed analyses of food quality, particularly involving nitrogen, would add a valuable potential mechanism to these breeding studies (White 2002).

Another important demographic variable that can influence mouse outbreaks is the breeding dynamics of mice in summer and autumn. The grain-growing region of south-eastern Australia is characterised by hot, dry summers. There is a marked reduction in breeding performance (percentage of adult females breeding and mean litter size) of mice from December to May (Singleton *et al*. 2001). Also, the breeding season may cease in late February or extend to June. Summer aridity may be an important limiting factor on breeding of mice (Mutze *et al*. 1991; Ylönen *et al*. 2003), with summer storms perhaps dampening the effect of aridity on breeding performance. The distribution of rainfall events in summer may be more important than total monthly rainfall measures. Also, summer rainfall would influence only the magnitude of an outbreak and provide only two months' warning for farmers.

It is clear that rainfall is indeed the driver of mouse outbreaks, but the exact causal pathway by which this is achieved is not yet clear, and once we understand the exact mechanisms by which rainfall operates, we will be able to increase the precision of these models and give farmers

advance warning of mouse outbreaks. Our results are in complete agreement with those of Brown and Ernest (2002) for rodents in the desert south-west of the USA. They found that the linkages from rainfall to rodents were more complex and less predictable than has been implied in simple models of desert rodent dynamics (Brown and Ernest 2002)

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