

Landscape ecology of house mouse outbreaks in south-eastern Australia

GRANT R. SINGLETON,*† COLIN R. TANN§ and CHARLES J. KREBS†‡

*International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines; †CSIRO Sustainable Ecosystems, GPO Box 284, Canberra, ACT 2601, Australia; ‡Department of Zoology, University of British Columbia, Vancouver, BC, Canada V6T 1Z4; and §CSIRO Entomology, PO Box 59 Narrabri, NSW, 2390, Australia

Summary

1. House mouse *Mus domesticus* outbreaks in the grain-growing areas of south-eastern Australia occur irregularly and may be local or widespread, covering thousands of square kilometres. All natural and agricultural habitats are occupied when house mouse numbers are high, and the question we addressed was whether we can distinguish source and sink habitats within these agricultural landscapes so that management practices can be better targeted.

2. Live-trapping on replicated grids in 15 habitats, including eucalypt woodland, cypress pine woodland, areas of permanent water and crop habitats, was carried out from 1983 to 1988 at 9-week intervals.

3. Agricultural cropland (including crops, fallow and pastures), farm buildings, seepage areas and natural woodland could be source habitats. Farm buildings, seepage areas and saltbush areas all had high mouse densities entering the 1983–84 outbreak and were refuge habitats for mice.

4. Cropland habitats quickly became the source area in spring 1983, and woodlands were initially sinks that lagged 2–4 months behind the population growth shown in crops.

5. Adult female mice in cropland habitats were more often in breeding condition compared with mice in natural woodland. Mice also had higher indices of residency in cropland than in natural woodland.

6. *Synthesis and applications.* In non-irrigated cereal production areas of south-eastern Australia, house mice move from refuge habitats in seepage areas and farm buildings into crops, build up in numbers in cropland habitats, and then invade woodland habitats, which by themselves cannot generate outbreaks of this pest species. Monitoring for incipient outbreaks should concentrate on refuges in seepage areas and crops and their associated fence lines as source habitat indicators. Population control in these habitats in spring would reduce the likelihood of population outbreaks in autumn, leading to reduced rodenticide use and a concomitant reduction in environmental hazards.

Key-words: Australia, house mice, *Mus domesticus*, outbreaks, refuge habitats, sink and source habitats

Journal of Applied Ecology (2007) **44**, 644–652

doi: 10.1111/j.1365-2664.2007.01296.x

Introduction

House mice *Mus domesticus* (Schwarz and Schwarz) have been a serious agricultural pest in the grain-

growing areas of south-eastern Australia for the last 100 years (Singleton *et al.* 2005). They have irregular outbreaks every 3–9 years, and rainfall is a key driving variable (Pech *et al.* 1999; Krebs *et al.* 2004). Like many small mammals that have periodic irruptions, people have often thought that the high numbers must have come from somewhere else and migrated into the local area (Singleton *et al.* 2003). Scandinavian

lemmings *Lemmus lemmus* are a legendary example (Stenseth & Ims 1993). Ecologists reformulated this idea at a landscape level with the concept of source and sink habitats (Pulliam 1988). Populations can persist and increase in source habitats because their average rate of increase is positive. Sink habitats obtain individuals by migration and, if isolated, the population in a sink habitat will become extinct because it cannot, on average, support a positive rate of growth.

In North America, the habitats generally used by mice are ephemeral and are linked to a 'fugitive' life-style (Anderson 1978). In the UK in commensal farm environments, mice aggregate in patches of suitable habitats and there is little dispersal between these patches. Survival is low but mice respond by breeding throughout the year (Pocock, Searl & White 2004). This life strategy is different from the seasonal breeding of mice in field environments (Berry 1968; Singleton *et al.* 2001).

In Australia, an understanding of habitat use by mice and their breeding dynamics in these habitats is important for providing an insight into how populations irrupt in agricultural landscapes (Newsome 1969b; Redhead & Singleton 1988; Singleton 1989; Twigg & Kay 1994; Jacob, Ylönen & Singleton 2004). This knowledge can be used to target when and where to manage mouse populations (Chambers, Singleton & van Wensveen 1996; Ylönen *et al.* 2002; Brown *et al.* 2004). The importance of source or 'donor' habitats (after Hansson 1977) for the persistence of mouse populations has been shown to be important, but only at a field scale (50–1000 ha) (Newsome 1969a; Singleton 1989; Mutze 1991). From these sites, mice invade 'reception' (after Hansson 1977) or 'impact' (Redhead & Singleton 1988) habitats when conditions are favourable. In Australia, these impact habitats are generally wheat fields, grain stores and intensive animal husbandry facilities (Caughley, Monamy & Heiden 1994).

House mice in western Victoria, Australia, have aperiodic outbreaks that cause major economic and social impacts on the rural community (Singleton & Redhead 1989; Caughley Monamy & Heiden 1994). Mice live in a landscape that can be broadly classified into four habitat types: farm buildings, cropland, natural woodland and natural vegetation along water courses. Native woodland vegetation occupies a significant area of western Victoria on lands that have not been cleared for agriculture. Each of these types of habitats can be broken down into more specific categories. We wanted to test four general hypotheses about the landscape nature of house mouse outbreaks in western Victoria.

1. House mice build up in areas of natural woodland vegetation and then invade agricultural croplands. Natural woodland areas are the source areas for outbreaks.
2. Mouse populations build up in agricultural fields and then invade the natural woodland landscapes. Croplands are the main source area.
3. Mouse populations remain in refuge habitats and colonize cropland when conditions are favourable.

Commensal refuge habitats, such as barns and seepage areas along water bodies, provide the source habitats for mice that colonize croplands, and croplands then act as source areas for natural woodland and generate outbreaks of mouse populations.

4. Cropland, natural woodland and farm buildings are all source areas for mouse outbreaks and the source–sink conceptual model does not apply well to this landscape except temporally. Sink habitats are temporal rather than spatial, so the same habitat can be a source in some months and a sink in other months.

We tested these four hypotheses with data from 15 habitats at 48 sites in western Victoria, spread over 1500 km², for the period 1983–88.

Methods

The study was located in the central mallee region of Victoria near Walpeup (35°08'S, 142°02'E). This agricultural region is characterized by an extensive strip of cereal-cropping land, with large areas of natural woodlands to the north and south (Fig. 1). Croplands contain narrow fence lines and road verges with grassy or native tree vegetation. Within cereal-growing areas, approximately 95% of the farm areas are cropped, with some fields in fallow every second year (or, in dry periods, 2 years of fallow and one year of cropping). Mouse populations in 15 habitats were trapped within this region, as described in Table 1. There were three replicates of 14 habitats and six replicates of the cropped areas, giving a total of 48 sites. They were grouped into five major habitat types. (i) Croplands included fields actually in crop, typically wheat or barley, stubble after crops have been harvested, fence lines (3–4 m wide) at the border with crops or pasture, and pastures. (ii) Farm buildings included barns and sheds, piggeries, and large silo areas in towns where bulk quantities of grain were stored before shipment. (iii) Natural habitats included extensive tracts of natural woodlands dominated by cypress pines *Callitris* sp., she-oaks *Casuarina* sp. and mallee eucalypts (Fig. 1), and road verges on average 10 m in width dominated either by grasses or trees. (iv) Saltbush was natural shrub vegetation on low-lying saline soils dominated by salt-tolerant plants. (v) Seepage areas included vegetation around farm dams, permanent lakes and reservoirs, and areas along the sides of major irrigation channels with permanent water.

Live-trapping for house mice was carried out on each of the habitats listed in Table 1. We used Longworth live-traps on 5 × 7 grids with 10-m spacing, and trapped for three consecutive nights. Sampling across the 48 sites took on average 7 weeks, and was followed by a 1–2-week interval before the next trapping session began. Each of the habitats was sampled 28 times over the 5.5-year study. When trap success was higher than 75%, we trapped for only two nights. Linear habitats, such as fence lines, were trapped with lines of 35 Longworth traps. Traps were cleared each morning, beginning at dawn. Each mouse was sexed, ear-tagged, weighed

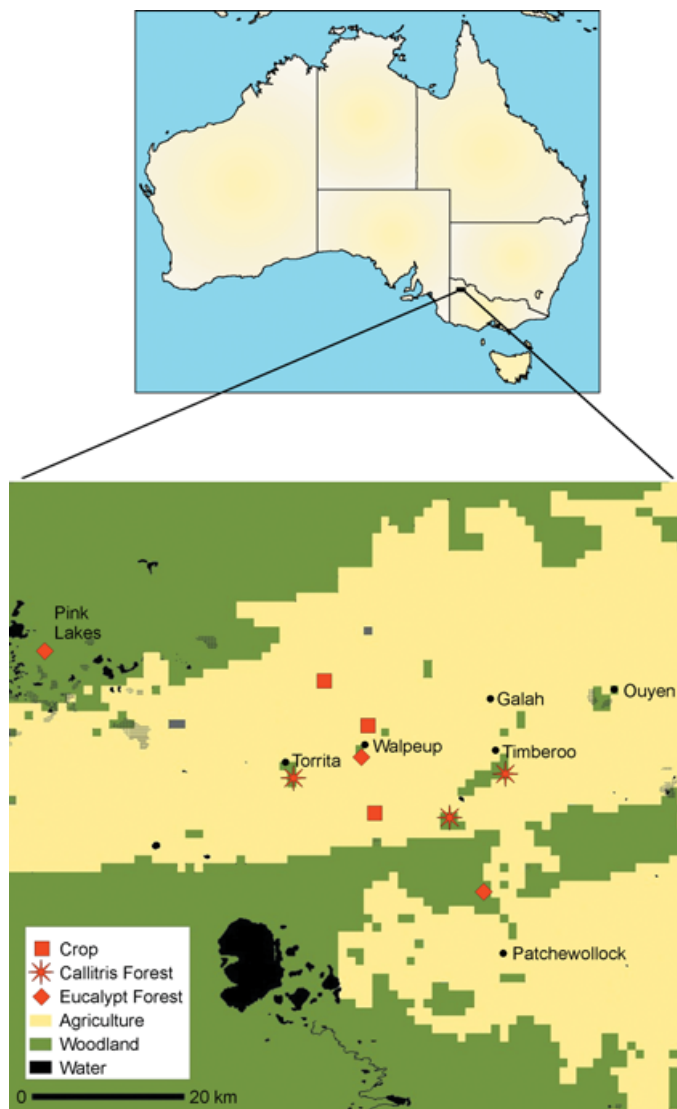


Fig. 1. Location of study areas in woodland and crop habitats in the central mallee region of Victoria, Australia (after Singleton *et al.* 2003). Most of the water areas are ephemeral salt lakes.

and its breeding condition noted, as described in Singleton (1983). All animals were released at the site of capture.

Because some habitats could be sampled only with lines of traps, we could not calculate mark–recapture estimates of density. We used the abundance index of number of mice caught per 100 trap nights, and adjusted this index for frequency by the method of Caughley (1977). For low and moderate densities of mice, this abundance index is closely related to the estimated population density of house mice from this part of Australia (Davis *et al.* 2003; C. J. Krebs, unpublished data). When the index exceeds 50–75 mice per 100 trap nights, the precision of the index falls because of the high variability associated with frequency measures as they approach 100%.

We interrogated the data using three criteria for source and sink populations: (i) habitats that show increases in mouse abundance earlier than others are source habitats; (ii) mice in source habitats should have higher reproductive rates than those in sink habitats, at any given point in time; (iii) mice in source habitats should have higher persistence (a combination of survival and remaining *in situ*) than mice in sink habitats when populations are low and increasing. The first criterion is a necessary and sufficient condition for a source, while at least one of either the second or third criteria is necessary to define a source population. We were concerned mainly with periods of low density and population increase rather than the period of rapid decline.

We defined refuge habitats as those where mice have high residency rates during non-breeding seasons, which is usually when there is a shortage of food and vegetative cover on average across the whole landscape. Mice moving out of refuge habitats can seed population growth in other habitats. Refuge habitats are not necessarily source habitats as defined above.

Table 1. General description of the 15 habitats trapped for house mice from March 1983 to March 1988 in the Walpeup region of western Victoria, Australia. There were three replicates of each habitat, except for crops where there were six

Habitat	Description
Crops	Fields actually in crop, from sowing through to harvest, mostly wheat
Fence line: crop	Fence row along the edges of a cropped field, 0.5–1 m wide, cropland on both sides
Fence line: pasture	Fence row with grazed stubble or pasture on both sides
Pasture	Burr medic <i>Medicago</i> sp., a major species, often sown in stubble paddocks; volunteer grass growth dependent on seasonal rainfall
Channel banks	Temporary earthen channels between dams with weedy cover
Farm buildings	Barns, main sheds and hay stores
Piggery	Buildings of various sizes housing pigs
Silo	Major grain storage areas in townships, typically for wheat or barley. These occur on average every 15 km along railway lines
Water verges	Edges of areas of permanent water, such as lakes and town water supplies
Road verge: grassy	Area between roads and fenced paddocks with grassy vegetation
Road verge: trees	Area between roads and fenced paddocks with mallee eucalypts, cypress pines <i>Callitris</i> sp. or she-oaks <i>Casuarina</i> sp.
<i>Callitris</i> woodland	Open woodland dominated by cypress pines
Eucalypt woodland	Open woodland dominated by species of eucalypts, typically mallee
Saltbush	Low-lying salt-pan areas dominated by salt-tolerant plants from the Chenopodiaceae
Seepage areas	Grass and weed areas along the main irrigation channels, usually moist and protected

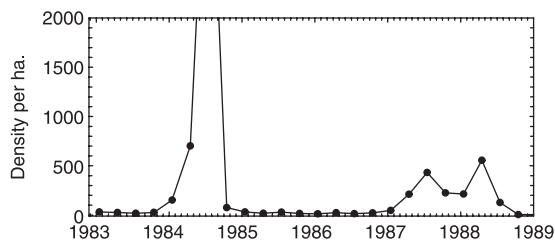


Fig. 2. Abundance of house mice in the Walpeup region of western Victoria from 1983 to 1989. Two outbreaks occurred during the time period of this study, a severe one in 1983–84, in which mouse densities reached more than 2000 ha⁻¹ in late summer, and a less severe outbreak in 1987 and 1988, in which densities reached about 500 ha⁻¹. Years indicate 1 January. Abundance is averaged over all habitats.

We present changes in abundance graphically with semi-log plots in which the slopes of the lines represent the rate of increase of the mouse population in that habitat. We use 90% confidence limits to indicate the relative precision of our estimates, basing the confidence limits on the Poisson distribution (Krebs 1999).

Because of small sample sizes within each individual habitat sample, data for each habitat group were pooled for statistical analyses. All statistical tests were carried out in NCSS Statistical Analysis Software (Kaysville, UT; www.ncss.com, accessed 7 March 2007).

Results

Two outbreaks of house mice occurred in western Victoria during the course of this study from 1983 to 1988 (Fig. 2). We divided this time series into three sections to look at the details of the outbreak build-up and the phase of low numbers in between outbreaks. We did not analyse the collapse of these outbreaks. In each case, the collapse occurred suddenly and simultaneously in all habitats (Pech, Davis & Singleton 2003).

AUTUMN AND WINTER 1983

The beginnings of the 1983–84 mouse outbreak could be identified in the relatively low abundance of mice over the winter of 1983. Figure 3 shows the estimated abundance of house mice in five habitats from April to August 1983. Over this period, house mice were nearly stationary in numbers or declined only slightly, and we can interpret these data as indicators of the abundance at the point of entering the 1983–4 breeding season in August. Mice were abundant in only one natural habitat, saltbush, and two commensal habitats. Farm buildings, including piggeries, contained the largest number of mice, with indices 15–25 times higher than those in cropland and woodland habitats. Seepage areas along permanent water bodies were also at relatively high density in the winter of 1983, with indices 10–15 times higher than those in crops and woodland.

Figure 4 shows the changes in abundance of mice over the winter and spring of 1983. Mouse numbers in natural

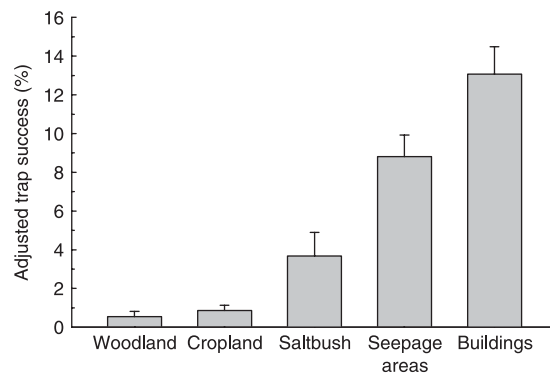


Fig. 3. Abundance of house mice in five major groups of habitat types in western Victoria from autumn through winter (April–August) in the lead up to the outbreak of 1983–84. Farm buildings include piggeries and silos as well as farm sheds.

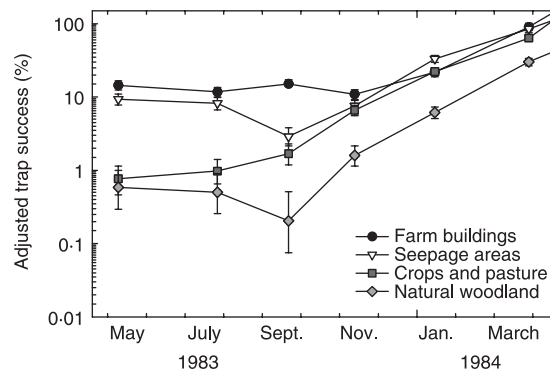


Fig. 4. Average abundance of house mice in four types of habitats in the increase phase of the 1983–84 outbreak. Mean adjusted trap success per 100 trap nights \pm 90% confidence limits. Grain crops are sown in May and June and harvested in November and December in this region of Australia.

woodland and along seepage areas declined by about 75% from May to September. Mouse numbers in farm buildings maintained their abundance, while mice in cropland doubled in abundance from winter to early spring.

SPRING AND SUMMER 1983–84:

THE INCREASE PHASE

The spring breeding season began in the first week of August 1983, an early start. The crop habitats led the increase during the early spring, while all other habitats either declined or remained stable (Fig. 4). These results support the hypothesis that crop habitats are a source area early in an outbreak. After September 1983, mouse numbers in nearly all habitats increased at the same rate, so that on the basis of rate of increase it was not possible to distinguish sources and sinks.

The percentage of adult females that were classified as pregnant or lactating did not differ significantly from habitat to habitat during the winter or spring of 1983 (Table 2). The difficulty of looking for differences in breeding patterns early in the increase phase of an outbreak is that sample sizes are low. For example, no

Table 2. Adult females classified as pregnant or lactating during the 1983–84 outbreak. The four habitat groupings show similar patterns of reproductive output in winter and spring 1983 but differ significantly in the summer of 1984. Letters indicate significant differences in subgroups. The probabilities for chi-squared contingency table tests for differences among the four habitat groupings are given on the bottom line

Habitat group	Winter 1983 (May–Aug.)		Spring 1983 (Sept.–Nov.)		Summer 1984 (Jan.–May)	
	No. adults	% pregnant or lactating	No. adults	% pregnant or lactating	No. adults	% pregnant or lactating
Cropland	3	33.3	29	62.1	268	28.7a
Natural woodland	3	33.3	7	42.9	80	43.7b
Farm buildings	68	41.2	65	56.9	173	26.6a
Seepage areas	22	27.3	39	64.1	153	35.3a,b
<i>P</i> -value		> 0.69		> 0.70		0.027

Table 3. Residency rates of house mice during the main breeding season of the 1983–84 and 1986–88 outbreaks, and the two winter periods of both outbreaks. The percentage of tagged individuals that were recaptured 8–9 weeks later at the next trapping session is a combined estimate of survival and residency. The probabilities for chi-squared contingency table tests for differences among the four habitat groupings are given on the bottom line. Significantly different subsets are indicated by letters

Habitat group	Breeding: summer 1983–84 increase phase		Breeding: summer 1986–87 increase phase		Winter (May–Sept.) 1984 decline phase		Winter (May–Sept.) 1987 decline phase	
	No. adults	% persisting	No. adults	% persisting	No. adults	% persisting	No. adults	% persisting
Cropland	315	11.8a	242	2.9a	3067	2.7a	2252	4.7a
Natural woodland	83	4.8b	96	11.5b	1711	7.5b	892	13.5b
Farm buildings	205	2.4b	229	15.3b	1771	7.6b	1822	13.0b
Seepage areas	173	7.5a,b	149	10.7b	2171	0.5c	1981	3.0a
<i>P</i> -value		0.000		0.000		< 0.0001		0.000

adult females were caught in September 1983 in woodland habitats, and thus we were not able to determine whether pregnancy rates differed between crops and natural woodlands at this critical part of spring breeding. In October and November 1983, pregnancy rates were 19% higher in crops than in natural woodlands, but because of a small sample size this difference was not statistically significant. What is striking in Table 2 is that breeding occurred at a high rate throughout the winter of 1983, when in a normal year there would be virtually no breeding activity (Singleton *et al.* 2001). Croplands, seepage areas and farm buildings showed overall higher breeding indices and were potential source habitats in spring 1983, whereas natural woodland was a potential sink habitat. Distinctions between source and sink areas tended to disappear in the summer of 1984, when all areas could be classed as productive sources. Female reproductive indices were 15% lower on cropland sites than they were on woodland area sites in the summer of 1984 ($P < 0.01$).

The designation of crop habitats as a source area was supported by the analysis of residency data (Table 3). Because residency (a combination of survival and remaining in the same home range) was always low over the 7-week interval between trapping rounds, we could not analyse it until populations were reasonable large. In mid-summer 1983–84, residency in crop habitats was significantly higher than that in other habitats, consistent with crops being source areas for

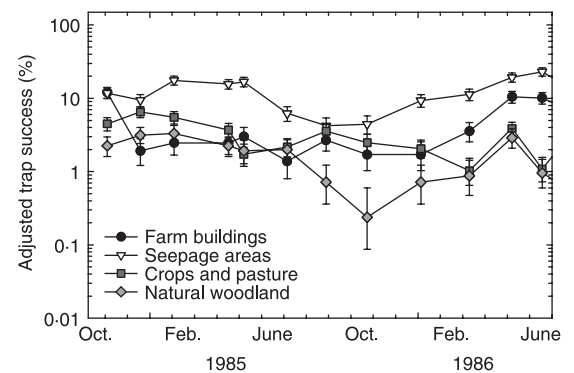


Fig. 5. Average abundance of house mice in four types of habitats in the low phase from 1984 to 1986. Mean adjusted trap success per 100 trap nights \pm 90% confidence limits.

mice. Later in the summer and autumn of 1984, after crops had been harvested, residency was lower in crop habitats, and the highest residency values occurred in natural woodland and seepage areas. Farm buildings always had low residency values.

SPRING AND SUMMER 1984–85 AND 1985–86: THE LOW PHASE

After the collapse of the 1983–84 outbreak, there were 2 years of low mouse numbers. There were relatively few population changes over this 2-year period (Fig. 5).

Table 4. Adult females classified as pregnant or lactating during the 1984–86 low phase breeding seasons, and the two spring breeding periods (August–October) of the second outbreak in 1986–88. The probabilities for chi-squared contingency table tests for differences among the four habitat groupings are given on the bottom line. Letters designate significant subsets

Habitat group	Breeding 1984–85 and 1985–86 combined (low phase)		Spring breeding 1986 (first year of outbreak)		Spring breeding 1987 (second year of outbreak)	
	No. adults	% pregnant or lactating	No. adults	% pregnant or lactating	No. adults	% pregnant or lactating
Cropland	89	56.2a	30	40.0	188	16.5
Natural woodland	28	28.6b	7	28.6	97	9.3
Farm buildings	91	15.4b	36	52.8	182	9.9
Seepage areas	191	65.5a	42	33.3	312	11.5
<i>P</i> -value		0.000		0.31		0.15

During the 1984–85 breeding period, all habitats showed essentially no population change or a slight decline. At the end of this breeding period, in early May 1985, mouse numbers were only 73% of what they had been at the start of breeding in all habitat types. Mouse numbers around seepage areas were highest, averaging 14% trap success, but still far below levels of the previous outbreak year, when the average trap success was 71%.

The winter of 1985 was a period of falling mouse numbers in natural woodland and seepage areas, although population abundance in cropland and farm buildings remained stationary.

During the 1985–86 breeding period, which began in early September and continued until early May 1986, mouse numbers increased about five-fold in all habitats except cropland, where numbers fell by about one-half (Fig. 5). By the end of this breeding season, numbers in all habitats were nearly the same as they were a year earlier, with an overall average trap success of 10–20% in farm buildings and seepage areas but only 1% in cropland and natural woodland. As breeding ended in June 1986 and the next outbreak was about to begin, the highest mouse populations were in farm buildings and seepage areas.

During the low period from 1984 to 1986, cropland habitats had a significantly higher percentage of females breeding than natural woodland habitats (Table 4) (56% vs. 29%, $\chi^2 = 6.49$, d.f. 1, $P = 0.01$). Mice from seepage areas had even higher reproductive indices (66%), while those from farm buildings had very low values (15%). These results are consistent with the hypothesis that cropland and seepage areas are potential source habitats.

Because recaptures of tagged mice were rare in periods of low numbers, residency values could not be analysed for the low phase from 1984 to 1986.

SPRING AND SUMMER 1986–87 AND 1987–88: THE SECOND OUTBREAK

The second house mouse outbreak during the 1980s was a 2-year outbreak in which numbers built up rapidly during 1986–87 and remained high, with a lesser increase from 1987 to 1988. Over the winter of

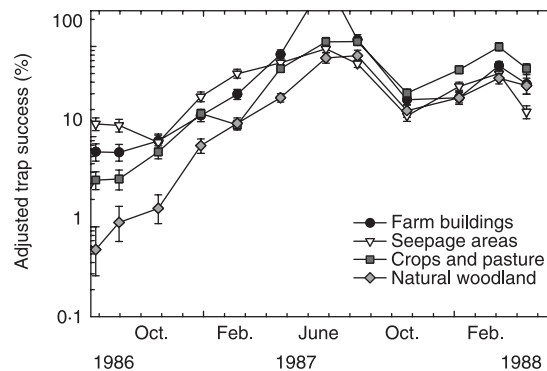


Fig. 6. Average abundance of house mice in four types of habitats in the mouse outbreak from 1986 to 1988. Mean adjusted trap success per 100 trap nights \pm 90% confidence limits.

1986 there was very little breeding, in contrast with the winter of 1983. No breeding females were captured in croplands or woodlands in the winter of 1986, and only 4% of adult females were pregnant in seepage areas and 7% in farm buildings over that winter. Consequently populations fell over this winter in all habitats.

The breeding season of 1986–87 began in mid-August and the populations in all habitats increased rapidly (Fig. 6). Populations in natural woodland began increasing at the same time as croplands, and from early August to October 1986 natural woodland populations increased three-fold while cropland populations increased two-fold. Only seepage areas differed in having a relatively low rate of increase, numbers increasing only five-fold over the breeding season, while the other habitats averaged an 18-fold increase in mouse abundance over the entire summer. We could detect no statistically significant differences in rates of increase in different habitats in spring or summer 1986–87.

Mice stopped breeding in May 1987, and numbers collapsed over the winter of 1987, with indices of abundance falling 70–80% in all habitats except farm buildings, where they fell even more (95%). The breeding season of 1987–88 began in mid-September and populations in all the habitats increased slowly (Fig. 6) until breeding ended in March 1988. Too few samples were taken to pinpoint the exact start of the population

increase in the different habitats. All habitats showed an identical two- to three-fold increase in mouse abundance, with cropland having the highest overall density and the highest rate of increase over the 1987–88 summer.

During the two spring breeding seasons of the second outbreak, female reproductive activity varied among habitats and between years but none of the differences was statistically significant (Table 4). In both breeding seasons during the second outbreak from 1986 to 1988, females in cropland had reproductive indices 7–11% higher than females in natural woodland, and cropland females were more abundant than females in natural woodland, but in neither case was this difference statistically significant. Reproductive indices were lower in spring 1987 (12% pregnant or lactating) than in spring 1986 (41%). The breeding data from the spring period of the second outbreak are consistent with the idea that crops are source habitats.

Residency rates in early summer of the second outbreak (Table 3) were low in crop habitats and higher in natural woodlands. This reversal of the pattern shown clearly in the 1983–84 outbreak can possibly be explained by the fact that crops had been already harvested in January 1987, and the suitability of cropland had declined. Unfortunately we did not have adequate data to measure residency in the early spring of 1986 (October–November) to determine whether this explanation for the anomaly was correct.

Discussion

The key question we addressed was whether we can recognize refuge, source and sink habitats for house mice in the agricultural area of western Victoria. In the time period before the 1983–84 outbreak, two refuge habitats were evident: farm buildings and seepage areas. An additional local refuge was saltbush habitat, but this habitat is not very extensive in western Victoria and consequently it cannot be of general regional importance. Farm buildings, including piggeries, were a classic, commensal refuge habitat for house mice. This is consistent with the landscape use of mice in agricultural areas in the northern hemisphere (Anderson 1978; Pocock, Searl & White 2004). In south-eastern Australian farms, seepage areas around water have also become refuges because they provide cover and food during droughts and other unfavourable periods, as recognized by Newsome (1969a). Mice moving out of refuge habitats can seed population growth in other habitats that are not uniformly favourable, but the exact quantitative importance of these habitats can only be estimated with a quantitative landscape model that is not yet available.

Mice were breeding throughout the winter of 1983, an unusual situation in these seasonal breeders (Singleton *et al.* 2001). The presumption is that this winter breeding was not sufficient to prevent a population decline in natural woodland and seepage area habitats, and only cropland habitats increased in density over this winter

period. Population growth that began in the late winter and early spring of 1983 was concentrated only in cropland habitats for 3 critical months, from August to October 1983. During this period cropland habitats could be recognized as source habitats, feeding mice out into surrounding areas. By late October 1983, mouse numbers were increasing in every habitat (Fig. 4) and there were no obvious source and sink habitats. Pregnancy and lactation rates were in fact slightly lower in cropland and farm buildings than they were in natural woodland and seepage areas, and at this time all habitats could be recognized as potential source habitats. However, the main breeding period in woodland habitats was 2 months later than in cropland habitats (Singleton *et al.* 2003). The increase in mouse numbers in woodland habitats in early September and October was clearly the result of mice moving there from surrounding croplands. Therefore natural woodland habitats were not important source habitats for the 1983–84 outbreak.

Once mouse numbers had collapsed over the winter of 1984, a 2-year low phase ensued. During the two breeding seasons that occurred during the low phase, croplands and seepage areas showed the highest reproductive indices for female mice, again indicating their potential importance as source areas. Over the 2-year period, abundance, as measured by trap success, was highest in seepage area habitats (12.5%) and considerably lower in croplands (3.2%) and natural woodland (1.7%). Farm buildings (4.6%) were similar or slightly higher in mouse abundance than croplands. We suggest that, over this low period, croplands and seepage areas served as source areas because of their higher reproductive output (Table 4). In particular, seepage areas appeared to be a significant refuge habitat in periods of low mouse abundance.

The second mouse outbreak of the late 1980s in western Victoria was not as severe as the earlier 1984 outbreak. Population growth in croplands and natural woodlands began before that in seepage areas, suggesting that either or both of these could have been potential source areas. But cropland females had the highest reproductive index, and reproductive rates were lower in natural woodland and delayed by about 7 weeks relative to crops, suggesting that crops were the source for mice moving into natural woodlands. Rates of population growth were similar in all habitats. In general, over the outbreak of 1987–88 there was a less striking division of habitats into sources and sinks, and the tendency of croplands to be a source habitat early in the outbreak, as shown in the 1983–84 outbreak, was less clear because of the difficulty of studying mice at very low densities.

CONCLUSION

Based on data from one major outbreak and one moderate outbreak, we can reject two of four hypotheses about the origin of mouse outbreaks in the mallee

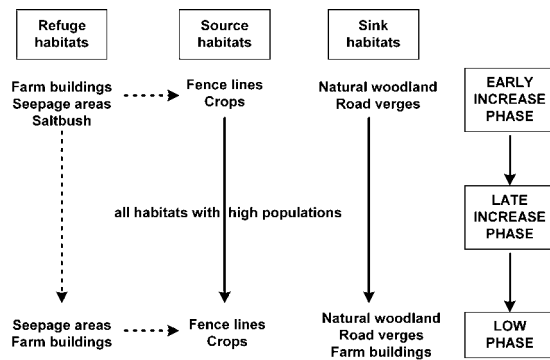


Fig. 7. Changes in refuge, source and sink habitats over the 1983–88 house mouse outbreaks in western Victoria. Most habitats maintain their status through an outbreak (except for the late increase phase) and retain that status even at low density. Refuge habitats occupy a very small fraction of the farming landscape in western Victoria (G. Singleton, personal communication), and their main contribution is to seed mice into source habitats (dotted lines) rather than provide demographic momentum to an outbreak.

region of western Victoria. Natural habitats were clearly not the source areas for the generation of these outbreaks. Seepage area and cropland habitats were the key source areas at the start of an outbreak. Just a few months after the start of an outbreak, all habitats had filled with mice and mice were breeding in all habitats at high rates (Table 2). Without cropland, we would predict that house mice could never generate an outbreak (Fig. 7). It is possible that seepage areas could serve as a natural source area, but these areas would be too small to produce enough individuals to populate the larger landscape habitats in the absence of cropland. Consequently we reject hypotheses 1 and 4.

The data support the third hypothesis, which postulates that mouse populations remain in refuge habitats during the low phase and colonize other habitats when conditions are favourable. Commensal habitats such as barns and piggeries serve as a potential source for the start of an outbreak, but this effect is short lived, and at best these commensal habitats are a temporary source sending mice into croplands. Croplands by themselves go through such boom–bust cycles that they alone cannot act as a refuge. For this reason, we reject hypothesis 2 as an adequate explanation of mouse outbreaks. We suggest that the third hypothesis is the best model of the landscape dynamics of mouse outbreaks. As a summary hypothesis, we suggest that mouse populations remain in refuge habitats and colonize croplands when conditions are favourable. Crops and their associated fence lines then serve as the main source of mice that move out to colonize other habitats such as road verges. This is consistent with findings from smaller farm-scale studies in various agricultural landscapes in Australia (Redhead, Enright & Newsome 1985; Singleton 1989; Mutze 1991; Twigg & Kay 1994; Ylönen *et al.* 2002). Commensal refuge habitats such as barns and seepage areas provide the sources of mice outbreaks (cf. Newsome 1969b). One prediction of this model is that extensive

areas of grain crops are essential to generate mouse outbreaks, a prediction consistent with the lack of outbreaks before 1900 (Mutze 1989; Singleton *et al.* 2005).

One way to test this model is to quantify it with parameters of landscapes in the mallee region of western Victoria. To do this we require estimates of the landscape contribution of all 15 habitats in the Walpeup region, and their spatial configuration. We believe that some habitats, such as piggeries and silos, while important locally, cannot operate as sufficient source habitats to drive mouse dynamics over large regions. We suggest that a landscape model would be a useful next step in understanding the dynamics of mouse outbreaks in south-eastern Australia. One prediction of such a model could be the amount of cropland that is required in a landscape to generate mouse outbreaks.

The consequences of a correct view of these landscape dynamics are important for resource managers, particularly farmers. An important finding is that mouse populations appear to build up within the farm habitats and not the natural woodland. This is the first time in Australia that mouse populations have been monitored longitudinally across such a wide range of natural habitats concurrently with agricultural habitats. Some farmers think that mouse populations build up in the natural woodland and then invade their crops. These farmers will not conduct early management on their properties because they do not perceive that they have ownership of the problem (Singleton *et al.* 2003). The findings of the present study should dispel that belief.

Current control recommendations for mouse outbreaks in Australia focus on a broad-scale use of rodenticides such as zinc phosphide. However, the use of rodenticides tends to be too late and requires large quantities to be distributed in late autumn and winter over areas of up to 500 000 ha (Brown, Chambers & Singleton 2002). The current study highlights that control along source habitats such as croplands in spring (August–October) would manage mouse populations before their numbers got too high, leading to reduced rodenticide use and a concomitant reduction in the environmental risks associated with rodenticides. Knowing when and where to control rodent populations is a necessary prerequisite for ecologically based rodent management (Singleton *et al.* 1999). Along these lines, Brown *et al.* (2004) has suggested a code of best farm practices for alleviating the impact of mouse outbreaks in this region, and these recommendations could be improved by ranking the relative importance of specific habitats for the generation of outbreaks. Monitoring for future mouse outbreaks should concentrate on crops and their associated fence lines as a key to population build-up in crops, seepage areas and, to a lesser degree, farm buildings as refuges.

Acknowledgements

We thank Pip Masters for her excellent technical assistance. Brian Coman and Trevor Redhead provided

critical appraisal of the design for this experiment and unerring encouragement. We also greatly appreciate the strong support of the farmers in the Victorian mallee wheatlands and the staff of the Mallee Research Station, particularly John Griffith and Geoffrey Stratford. The research was supported by the Grains Research and Development Corporation (CS44). We thank Roger Pech and Peter Brown for their critical reviews of the manuscript.

References

- Anderson, P.K. (1978) The serendipitous mouse. *Natural History*, **87**, 38–43.
- Berry, R.J. (1968) The ecology of an island population of the house mouse. *Journal of Animal Ecology*, **37**, 445–470.
- Brown, P.R., Chambers, L.K. & Singleton, G.R. (2002) Pre-sowing control of house mice (*Mus domesticus*) using zinc phosphide. Efficacy and potential non-target effects. *Wildlife Research*, **29**, 27–37.
- Brown, P.R., Davies, M.J., Singleton, G.R. & Croft, J.D. (2004) Can farm-management practices reduce the impact of house mouse populations on crops in an irrigated farming system? *Wildlife Research*, **31**, 597–604.
- Caughley, G. (1977) *Analysis of Vertebrate Populations*. Wiley, London, UK.
- Caughley, J., Monamy, V. & Heiden, K. (1994) *Impact of the 1993 Mouse Plague*. Occasional Paper Series No. 7. GRDC, Canberra, Australia.
- Chambers, L.K., Singleton, G.R. & van Wensveen, M. (1996) Spatial heterogeneity in wild populations of house mice (*Mus domesticus*) on the Darling Downs, southeastern Queensland. *Wildlife Research*, **23**, 23–38.
- Davis, S.A., Akison, L.K., Farroway, L.N., Singleton, G.R. & Leslie, K.E. (2003) Abundance estimators and truth: accounting for individual heterogeneity in wild house mice. *Journal of Wildlife Management*, **67**, 634–645.
- Hansson, L. (1977) Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. *Oikos*, **29**, 539–544.
- Jacob, J., Ylönen, H. & Singleton, G.R. (2004) Spatial distribution of feral house mice during a population eruption. *Ecoscience*, **11**, 16–22.
- Krebs, C.J. (1999) *Ecological Methodology*, 2nd edn. Addison-Wesley Longman Inc., Menlo Park, CA.
- Krebs, C.J., Kenney, A.J., Singleton, G.R., Mutze, G., Pech, R.P., Brown, P.R. & Davis, S.A. (2004) Can outbreaks of house mice in south-eastern Australia be predicted by weather models? *Wildlife Research*, **31**, 465–474.
- Mutze, G.J. (1989) Mouse plagues in south Australian cereal-growing areas. I. Occurrence and distribution of plagues from 1900 to 1984. *Australian Wildlife Research*, **16**, 677–683.
- Mutze, G.J. (1991) Mouse plagues in south Australian cereal-growing areas. III. Changes in mouse abundance during plague and non-plague years, and the role of refugia. *Wildlife Research*, **18**, 593–604.
- Newsome, A.E. (1969a) A population study of house-mice temporarily inhabiting a south Australian wheatfield. *Journal of Animal Ecology*, **38**, 341–359.
- Newsome, A.E. (1969b) A population study of house-mice permanently inhabiting a reed-bed in south Australia. *Journal of Animal Ecology*, **38**, 361–377.
- Pech, R.P., Davis, S.A. & Singleton, G.R. (2003) Outbreaks of rodents in agricultural systems: pest control problems or symptoms of dysfunctional ecosystems? *Rats, Mice and People: Rodent Biology and Management* (eds G.R. Singleton, L.A. Hinds, C.J. Krebs & D.M. Spratt), pp. 311–315. Australian Centre for International Agricultural Research, Canberra, Australia.
- Pech, R.P., Hood, G.M., Singleton, G.R., Salmon, E., Forrester, R.I. & Brown, P.R. (1999) Models for predicting plagues of house mice (*Mus domesticus*) in Australia. *Ecologically Based Management of Rodent Pests* (eds G.R. Singleton, L.A. Hinds, H. Leirs & Z. Zhang), pp. 81–112. Australian Centre for International Agricultural Research, Canberra, Australia.
- Pocock, M.J.O., Searl, J.B. & White, P.C.L. (2004) Adaptations of animals to commensal habitats: population dynamics of house mice *Mus musculus domesticus* on farms. *Journal of Animal Ecology*, **73**, 878–888.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.
- Redhead, T.D. & Singleton, G.R. (1988) The PICA strategy for the prevention of losses caused by plagues of *Mus domesticus* in rural Australia. *EPPO Bulletin*, **18**, 237–248.
- Redhead, T.D., Enright, N. & Newsome, A.E. (1985) Causes and predictions of outbreaks of *Mus musculus* in irrigated and non-irrigated cereal farms. *Acta Zoologica Fennica*, **173**, 123–127.
- Singleton, G.R. (1983) The social and genetic structure of a natural colony of house mice, *Mus musculus*, at Healesville wildlife sanctuary. *Australian Journal of Zoology*, **31**, 155–166.
- Singleton, G.R. (1989) Population dynamics of an outbreak of house mice (*Mus domesticus*) in the mallee wheatlands of Australia: hypothesis of plague formation. *Journal of Zoology (London)*, **219**, 495–515.
- Singleton, G.R. & Redhead, T.D. (1989) House mouse plagues. *Mediterranean Landscapes in Australia: Mallee Ecosystems and Their Management* (eds J.C. Noble & R.A. Bradstock), pp. 418–433. CSIRO, Melbourne, Australia.
- Singleton, G.R., Brown, P.R., Pech, R.P., Jacob, J., Mutze, G.J. & Krebs, C.J. (2005) One hundred years of eruptions of house mice in Australia: a natural biological curio. *Biological Journal of the Linnean Society*, **84**, 617–627.
- Singleton, G.R., Hinds, L., Leirs, H. & Zhang, Z. (1999) *Ecologically Based Management of Rodent Pests*. Monograph No. 59. Australian Centre for International Agricultural Research, Canberra, Australia.
- Singleton, G.R., Kenney, A.J., Tann, C.R. & Sudarmaji & Hung, N.Q. (2003) Myth, dogma and rodent management: good stories ruined by data? *Rats, Mice and People: Rodent Biology and Management* (eds G.R. Singleton, L.A. Hinds, C.J. Krebs & D.M. Spratt), pp. 554–560. Australian Centre for International Agricultural Research, Canberra, Australia.
- Singleton, G.R., Krebs, C.J., Davis, S., Chambers, L. & Brown, P. (2001) Reproductive changes in fluctuating house mouse populations in southeastern Australia. *Proceedings of the Royal Society of London Series B*, **268**, 1741–1748.
- Stenseth, N.C. & Ims, R.A. (1993) *The Biology of Lemmings*. Academic Press, London, UK.
- Twigg, L.E. & Kay, B.J. (1994) The effects of microhabitat and weather on house mouse (*Mus domesticus*) numbers and the implications for management. *Journal of Applied Ecology*, **31**, 651–663.
- Ylönen, H., Jacob, J., Davies, M. & Singleton, G.R. (2002) Predation risk and habitat selection of Australian house mice (*Mus domesticus*) during an incipient plague. Desperate behaviour due to food depletion. *Oikos*, **99**, 284–289.

Received 29 March 2006; final copy received 17 January 2007
Editor: Chris Dickman