



# Conservation agriculture practices have changed habitat use by rodent pests: implications for management of feral house mice

Wendy A. Ruscoe<sup>1</sup> · Peter R. Brown<sup>1</sup> · Steve Henry<sup>1</sup> · Nikki van de Weyer<sup>1</sup> · Freya Robinson<sup>1</sup> · Lyn A. Hinds<sup>1</sup> · Grant R. Singleton<sup>2</sup>

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## Abstract

The advent of ‘conservation agriculture’ (CA) farming using zero- or no-tillage practices and an accompanying change in crop rotations in the last 10–15 years has potentially led to less disturbance of mouse burrows and increased cover and food supply. Given the irregular outbreaks of mice in grain cropping regions in Australia and the damage they cause, it is important to understand when and where mouse populations increase so that management strategies can be improved. We utilised a 20-year long-term mouse population data set collected prior to the introduction of CA farming practices and a more recent 8-year data set after CA to compare changes in mouse population abundance in a typical dryland grain cropping system in north-western Victoria, Australia. Mouse trapping data were used to compare abundance in crop and margin habitats during crop growth and non-crop (fallow) periods before (‘conventional’) and after introduction of CA. Mice are now resident year-round within crops and stubble and appear to only spill over into margin habitats. Previously developed recommendations for mouse management that include their control while in margin habitats may no longer be valid.

**Keywords** No-till · Disturbance · Ecology · Rodent pest management · *Mus musculus domesticus* · Behaviour

## Key Message

- Conservation agriculture farming systems have changed the way mice utilise different habitats in and around cropped fields.
- Mice no longer use crop-margin habitats as refuges or use these habitats as ‘donor’ habitats to reinvade crops.
- Mice are now resident within crops and stubble, and only spill over into margin habitats.
- Recommendations for mouse management that include their control while in margin habitats are no longer valid.

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✉ Wendy A. Ruscoe  
wendy.ruscoe@csiro.au

<sup>1</sup> Health and Biosecurity, Commonwealth Scientific and Industrial Research Organisation (CSIRO), GPO Box 1700, Canberra, ACT 2601, Australia

<sup>2</sup> Natural Resource Institute, University of Greenwich, Chatham Maritime, Kent, UK

## Introduction

A consequence of the ever-increasing global human population is the requirement for increased food production through increased crop yields (Tilman et al. 2011). Coincident with this need are concerns to reduce the impact of increasingly intensive agriculture on biodiversity (Tilman et al. 2011), carbon sequestration (Smith et al. 2005), soil erosion and water retention (Bescansa et al. 2006; Soane et al. 2012) and greenhouse gas emissions (Vermeulen et al. 2012). One approach to achieve these multiple aims is through the use of conservation agriculture (CA) practices which are considered to be more environmentally sensitive and economically viable than conventional systems (Soane et al. 2012). Increasingly used conservation practices in broadacre dryland cereal production include no- and zero-tillage: seeds are directly drilled into the soil with minimal soil disturbance, accompanied with retaining crop stubble, usually treated with herbicide prior to seeding. In addition to providing protection against erosion, CA improves soil health and resilience by preserving beneficial soil structure, improving moisture storage and organic matter, and enhancing habitat for diverse soil micro- and meso-fauna (Kertész

and Madarász 2014). However, there are unintended consequences emerging with CA, such as the increased incidence of pests, particularly rodents. For example, when the ground is not ploughed each year, and intact burrow systems and crop residues are maintained, the potential exists for substantial increases in pest rodent populations (Heroldová et al. 2018; Witmer et al. 2007) with subsequent crop damage (Johnson 1987). It is therefore important to understand how and when pest rodents use different habitats and how this can assist with development and implementation of management strategies to reduce their impact.

Cropping landscapes result from the removal and fragmentation of natural habitats, leading to large expanses of monoculture interspersed with uncultivated areas such as fence lines, field margins or strips along watercourses and roads. Often, these uncultivated habitats contain small mammals, which when present in high numbers can infiltrate crops causing crop damage and economic losses (Brown et al. 2007; Jacob and Tkadlec 2010; Leirs et al. 2010; Singleton et al. 2010; Stenseth et al. 2003; Witmer and Proulx 2010). In addition, conventional farming practices typically cause disturbance making cropping paddocks temporally unfavourable for rodents. For example, crop harvesting results in a sudden decrease in cover thereby making animals more susceptible to predation effects; either real or perceived (Arthur et al. 2004; Bonnet et al. 2013; Jacob 2003; Jacob and Hempel 2003; Ylonen et al. 2002). Post-harvest ploughing can destroy burrows, kill animals and bury any remaining food and weed plants (Jacob 2003). Additionally, both conventional and CA cropping result in large, synchronised fluctuations in food supply at the paddock scale.

Perturbations such as those associated with agricultural landscapes act as ecological filters selecting for ‘fugitive’ species, i.e. species able to colonise and reproduce fast enough to renew populations before an adverse change occurs (Ronce et al. 2000). Highly mobile species, like small mammals, can respond to habitat perturbation by reallocating their daily activities among different habitats within their individual home ranges or by shifting to other habitats (Bonnet et al. 2013). These traits have also been referred to as part of the coloniser syndrome (after Baker and Stebbins (1965)) or part of the ‘ruderal strategy’ (Grime 1977). This has led to the study of the importance of stable refuge habitats (uncultivated areas) within agricultural lands for the persistence of pest animals and for understanding their population processes (Bonnet et al. 2013; Rodríguez-Pastor et al. 2016; Singleton and Redhead 1990; Witmer et al. 2007) when crop fields are unfavourable.

In Australia, the introduced house mouse (*Mus musculus domesticus*) uses refuge areas or ‘donor’ habitats, such as reed beds, fence lines, road verges, and grassed banks of dams, in grain growing regions (Mutze 1991; Singleton et al. 2007). These habitats have been particularly important

following crop harvest when paddocks were routinely ploughed (tilled) changing vast areas of cropland from favourable to inhospitable for mice. From these donor habitats, mice are thought to reinvade the new crop when there is increased vegetative cover and food (seeds/grains) during the growing season. This information formed the basis of management recommendations that farmers were encouraged to follow (Brown et al. 2004, 2010). Management actions have included mowing, burning, herbicide application, and the use of rodenticides to control pest populations while they are in these restricted parts of the landscape (Brown et al. 2004; Witmer et al. 2007; Ylonen et al. 2002, 2003).

Plagues of mice have been recorded in the winter cereal cropping regions of Australia over the last 120 years causing significant economic damage (Brown et al. 2007; Singleton et al. 2005). Prior to the uptake of CA, a 20-year study (1983–2002) of mouse populations at Walpeup, Victoria, in south-eastern Australia provided detailed knowledge of their breeding ecology, demographic changes, spatial behaviour and epidemiology (Singleton et al. 2005). Rainfall and habitat characteristics via their effects on food supply, availability of nesting sites, and protection from predators have emerged as important factors that influence mouse population dynamics (Arthur et al. 2003a; Brown and Singleton 1999; Krebs et al. 2004; Singleton et al. 2001; Singleton 1989). Winter rainfall has been shown to be a good predictor of summer rate of population increase while the winter population decline is heavily density dependent (Davis et al. 2003). The recent change (< 20 years) to CA cropping practices, however, requires a reassessment of both mouse population dynamics and management recommendations.

Long-term studies of mouse abundance and habitat use provide an opportunity to examine whether mice have changed their habitat use in the CA farming system compared to the earlier ‘conventional’ farming system. Studies have been conducted on grain farms in and around the Walpeup region of north-western Victoria (Victorian Mallee), Australia from 1983 to 2002 (Singleton et al. 2005), and routine monitoring recommenced from 2012 through to 2020, thus covering two discrete periods with different farming systems. Results from farmer surveys in this region show that CA practices were virtually absent in 1980, rising to only 30% of farmers by 2002 (Llewellyn and D’Emden 2010; Llewellyn et al. 2012). During this time the regular ploughing of paddocks probably exacerbated the importance of non-crop refuges for mice. Adoption of CA techniques increased rapidly after this time with around 80% farmers using zero- or no-till practices in 2008 (Llewellyn and D’Emden 2010; Llewellyn et al. 2012) indicating a substantial shift in agricultural land use. Singleton and Brown (1999) postulated that changes in farming practices associated with CA adoption in Australia would lead to less disturbance of mouse nesting sites in paddocks and longer food

availability (spilled grain not being buried by ploughing), and could result in higher frequencies of population eruptions. This hypothesis has not yet been tested.

By comparing mouse trapping data from the ‘historic’ (1983–2002) and ‘recent’ (2012–2020) periods we assess how the change in cultivation practices may have changed landscape use by mice. Specifically, we want to know if the use of margin habitats (fence lines and unmanaged roadside verges which were trapped during both the historic and recent data collection periods) during the post-harvest season (a 5–6 month interval between crop harvest and re-sowing) has changed since the introduction of CA. We also test whether changes in cultivation practices have changed the underlying population dynamics of this irruptive pest. While acknowledging the lack of a strict experimental design with simultaneous treated and untreated areas, we used comparable data to test the following predictions:

**Hypothesis 1** The main drivers related to the irruptive nature of mouse populations in our study area have not changed between the historic and recent data collection periods.

**Hypothesis 2** Trap success decreased in paddocks and increased on crop-margins during the non-crop (fallow) season during the historic data collection period (1983–2002) as disturbance caused by ploughing destroyed burrows, buried spilled grain and weeds, and reduced vegetative cover.

**Hypothesis 3** Trap success does not decrease in paddocks and increase on margins during the non-crop period during the recent CA data collection period (2012–2020) as burrows were not disturbed, spilled grain remained on the soil surface, and standing stubble provided cover.

**Hypothesis 4** Trap success remained high in paddocks in the non-crop season during the recent period (2012–2020) compared to the historic period (1983–2002) as mice are not forced out of the paddocks following harvest under CA practices.

## Methods

### Study area

The study was conducted within 5 km of the Mallee Research Station at Walpeup, Victoria, Australia (35°08' S, 142°02' E) on typical grain farms growing winter wheat, barley and legume crops. Planting of crops occurred in autumn (April or May) and harvesting occurred in summer (late November and December). The area has an average yearly rainfall of 335 mm. More rain falls in winter and is less variable (May–Aug, mean = 130 mm, CV = 39%) than

in summer (Jan–Apr, mean = 89 mm, CV = 63%). For the other four months (Sep–Dec) on average 118 mm falls with a CV of 50%. Rainfall records were obtained from the Mallee Research Station.

### 1983–2002: Historic data—conventional cropping

The historic data were from capture-mark-recapture monitoring of free-living mice over 20 years by CSIRO (1983–2002; Singleton et al. 2005). The exact locations of the trapping sites changed four times over the course of the study but were all around the township of Walpeup in similar crop land.

During each monitoring session, mouse trapping was conducted in paddocks and in non-crop habitats using Longworth live-capture small mammal traps (Longworth Scientific, Abingdon, UK). For this analysis we used data from trapping grids in paddocks either under crop or as a stubble (grids ranged from 5 × 5 to 7 × 7 traps at 10 m spacing) and from trap lines along margin habitats on within-farm fence lines and along roadside verges (10–30 traps at 10 m spacing). The paddocks that were cropped were typically 50 to 100 ha.

The trapping protocol remained essentially the same throughout the study although the number of trapping nights (2–10 nights) and number of traps (10–49 traps per grid or trap line) per session did change. All animals trapped were individually marked and released at point of capture. See Singleton (1989) for trapping protocol details. For comparison with recent data, we calculated trap success as the number of individual mice trapped per 100 trap nights set in paddocks (crops and stubble) and margins (fence lines and roadside verges) for each trapping session over the 20-year period. Trap success was modified to correct for trap saturation (Leslie and Davis 1939) as suggested by Caughley (1977) and standardised to an adjusted trap success per 100 trap nights (ATS).

$$ATS = 100 * -\ln\left(1 - \frac{\text{number of individual mice trapped}}{\text{number of traps set}}\right)$$

### 2012–2020: Recent data: conservation agriculture

Trapping was conducted on a typical grain farm within 5 km of the Mallee Research Station over an 8-year period. Trapping occurred in autumn, winter and spring in two paddocks and along two fence lines—one between the two paddocks and one between a paddock and remnant woodland. There was a 3-year crop rotation with a cereal (mainly wheat, but some barley), followed by canola, then a legume. There was no grazing or fallow phase, post-harvest weeds were controlled using herbicide and the soil was not ploughed prior

to sowing. Mice were trapped using Longworth live capture small mammal traps (Longworth Scientific, Abingdon, UK) spaced 10 m apart on 6 × 6 grids in the paddocks. On each fence line, 15 traps were placed at 10 m intervals. All trapping sessions were 3 nights and animals were marked to identify capture, but they were not uniquely marked. As with the historic data, an adjusted trap success was calculated for each paddock and margin habitat.

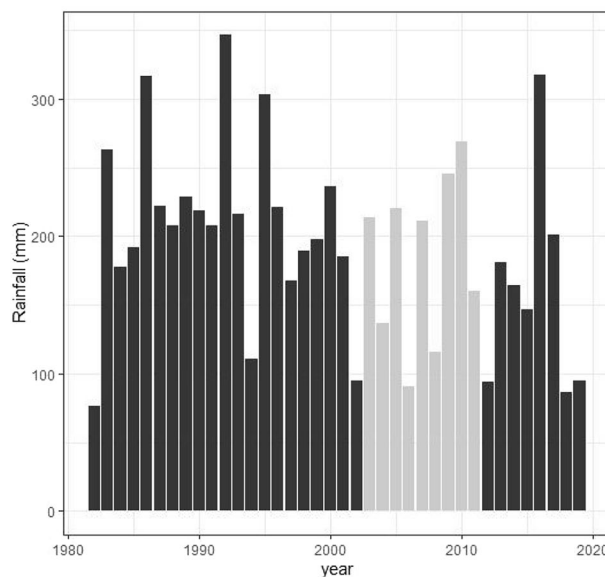
### Analysis of population dynamics

Trapping occurred in different months in different years but there was always a spring trapping session when crops were producing grain and mouse breeding was occurring, and an autumn trapping session prior to sowing the following year. For each ‘crop year’ (April<sub>*t*</sub> – March<sub>*t+1*</sub>) trapping sessions were identified as occurring during the ‘crop-growing season’ or ‘non-crop season’. The crop growing season was defined as the spring period from September to November when the crop was high (tillering to maturation) and before harvest. The non-crop season was defined as January to May when paddocks were in stubble (after harvest and before sowing of the next crop). Trap success from each paddock trapped during these seasons were averaged to obtain a mean trap success (*ATS*) per crop season (crop and non-crop season) within a crop-year, in each habitat (paddock vs margin) separately. Data from other months were not used as sowing time in an individual paddock could occur anytime from April to June. Harvest was generally in December, but the December trapping session could have been before or after harvest in any particular paddock.

Previous analysis of the historic data have shown that house mouse populations have seasonal changes in abundance where rainfall positively correlates with the rate of increase during the breeding season, while the density at the end of breeding (late summer/autumn) affects the decline over the non-breeding season (Davis et al. 2003; Kenney et al. 2003).

Instantaneous rates of change in mouse density between crop seasons ( $r_t$ ) were estimated from sequential mouse trap success rates as  $r = \text{Log}_e(\text{ATS}_{t+1}) - \text{Log}_e(\text{ATS}_t)$ , where  $t$  (months) was the transition between the Crop Season (spring) population lows and Non-Crop season (autumn) population peaks.

We used linear regression models in R (R Core Team 2020) to examine whether these same population drivers were operating in the recent data set (Predictions H1 & H2). We modelled rate of population increase ( $r_{\text{increase},i}$ ) from the spring population low to the autumn population high each cropyear ( $i$ ) as a linear function of rainfall (cumulative total 1 April–31 October each year) and the period (Historic or Recent) the data came from.



**Fig. 1** The sum of April to October rainfall at the Mallee Research Station over the study periods (historic conventional cropping, 1982–2002, and recent conservation agriculture cropping, 2012–2020). Rainfall data for 2003–2011 are shown in grey bars for reference. No mouse trapping occurred in those years but there was a mouse outbreak in 2011 following the break of the millennium drought in 2010

$$r_{\text{increase},i} \sim \alpha_0 + \alpha_1 \text{Period}_i + \alpha_2 \text{Rainfall}_i + \alpha_3 \text{Period}_i, \text{Rainfall}_i + \varepsilon_i \quad (\text{Model A})$$

where  $\alpha_0$  is the intercept,  $\alpha_1$  is the coefficient estimating the effect of period on rate of increase,  $\alpha_2$  is the coefficient estimating the effect of rainfall,  $\alpha_3$  is the interaction effect for period and rainfall, and  $\varepsilon_i$  is the residual error.

We modelled the rate of population decrease ( $r_{\text{decrease},i}$ ) from the autumn population high to the spring population low (winter crash) as a linear function of adjusted trap success (*ATS*) in autumn and the period the data came from.

$$r_{\text{decrease},i} \sim \beta_0 + \beta_1 \text{Period}_i + \beta_2 \text{ATS}_i + \beta_3 \text{Period}_i, \text{ATS}_i + \varepsilon_i \quad (\text{Model B})$$

where  $\beta_0$  is the intercept,  $\beta_1$  is the coefficient estimating the effect of period on rate of increase,  $\beta_2$  is the coefficient estimating the effect of adjusted trap success in autumn,  $\beta_3$  is the interaction effect for period and adjusted trap success, and  $\varepsilon_i$  is the residual error.

### Habitat comparison

The data were analysed using a linear mixed effect models using the lmer function in the lme4 package (Bates et al. 2015) in R (R Core Team 2020). The data were modelled with PERIOD (Historic vs. Recent), SEASON (Crop vs Non-Crop) and HABITAT (Paddock vs Margin) as fixed effects and crop-year as a random effect that takes into

account the large differences between the 28 individual years (outbreak and non-outbreak years). Trap success data were transformed ( $Y_j = \log_e(ATS_j + 1)$ , where  $Y_j$  is the natural log transformed mean  $ATS$  for year  $j$ ) to normalise it and account for real zeros in the data. Residual plots indicated that this was appropriate. Adjusted Akaike Information Criterion (AICc) was used to compare models (Burnham and Anderson 2002). Figures were produced using the packages ggplot2 (Wickham 2009), ggeffects (Ludecke 2018) and patchwork (Pedersen 2020) in R. Outbreak and non-outbreak years have been graphed separately as grouping them leads to very large standard errors obscuring real differences.

While paddocks were being conventionally cropped (Historic Period), the paddock soil was routinely tilled during the non-crop fallow season prior to crop sowing, forcing mice to leave the Paddocks and seek refuge in undisturbed Margins (fence lines and verges). As such we would expect a shift from high to low trap success in Paddock Habitat in the Non-Crop Season; a significant SEASON × HABITAT interaction in Model C (Prediction H2).

$$Y_i \sim \gamma_0 + \gamma_1 \text{Habitat}_i + \gamma_2 \text{Season}_i + \gamma_3 \text{Habitat}_i, \text{Season}_i + \gamma_i + \varepsilon_i \quad (\text{Model C})$$

where  $Y_i$  is the overall mean population size in cropyear  $i$ ,  $\gamma_1$  is the coefficient estimating the effect of habitat on population size,  $\gamma_2$  is the coefficient estimating the effect of season on population size,  $\gamma_3$  is the interaction effect for habitat and season,  $\gamma_{\text{cropyear}}$  is the random effect of cropyear on the intercept, and  $\varepsilon_i$  is the residual error.

Under CA (Recent Period), soil is not disturbed, and the stubble and spilt grain is left on the ground following harvest, with the consequence of retaining burrows, food supply and cover for mice in the Paddocks. As such, mice are not forced to move from Paddocks to Margin Habitat following harvest so we would *not* expect a HABITAT × SEASON interaction in Model C (Prediction H3).

If paddock disturbance forces mice from Paddocks to Margin Habitat during the Non-Crop Season in the Historic Period but not the Recent period, we expect this to be reflected in a HABITAT × SEASON × Period interaction in trapping data (Model D, Prediction H4).

$$Y_i \sim \varphi_0 + \varphi_1 \text{Habitat}_i + \varphi_2 \text{Season}_i + \varphi_3 \text{Period} + \varphi_3 \text{Habitat}_i, \text{Season}_i + \varphi_4 \text{Habitat}_i, \text{Period}_i + \varphi_5 \text{Season}_i, \text{Period}_i + \varphi_6 \text{Habitat}_i, \text{Season}_i, \text{Period}_i + \varphi_i + \varepsilon_i \quad (\text{Model D})$$

where  $Y_i$  is the overall mean population size in cropyear  $i$ ,  $\varphi_1$  is the coefficient estimating the effect of habitat on population size,  $\varphi_2$  is the coefficient estimating the effect of season on population size,  $\varphi_3$  is the coefficient estimating the effect of period on population size,  $\varphi_4$  is the interaction

effect for habitat and period,  $\varphi_5$  is the interaction effect for season and period,  $\varphi_6$  is the 3-way interaction effect for habitat, season and period,  $\varphi_{\text{cropyear}}$  is the random effect of cropyear on the intercept, and  $\varepsilon_i$  is the residual error.

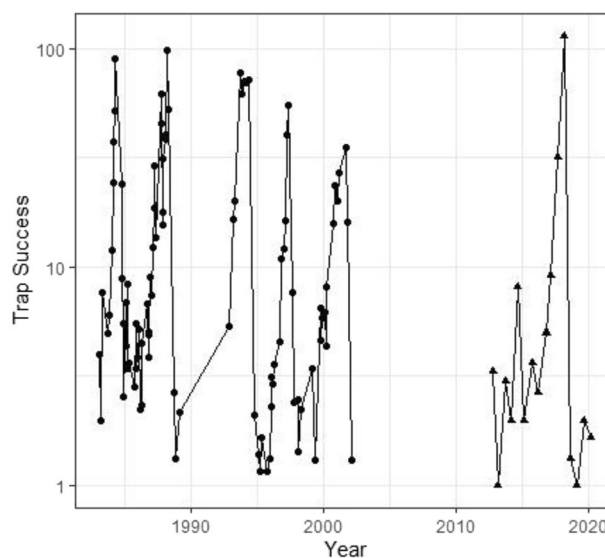
## Results

### Population trends

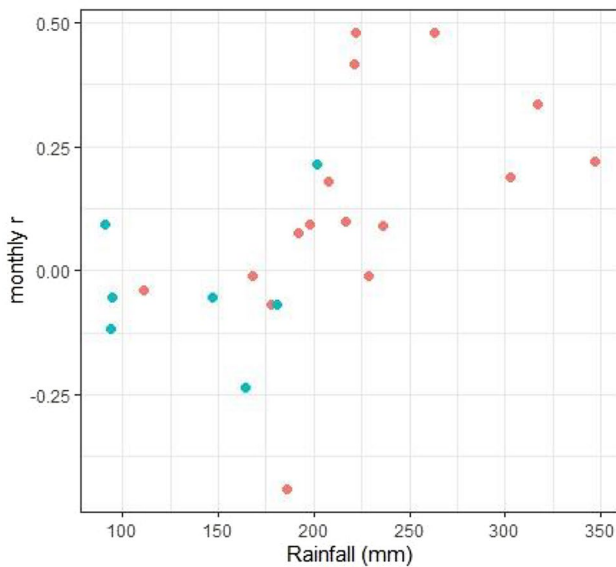
House mice in the Mallee grain cropping area experienced five outbreaks (two spanning two years) between 1983 and 2002 (Singleton et al. 2005). There was another outbreak in 2018 similar in magnitude to previous outbreaks (Fig. 2). During non-outbreak years, populations were very low and sometimes undetectable.

Higher rates of population increase were associated with higher rainfall years ( $F_{1,21} = 5.07, P = 0.006$ ; Fig. 3). Adding Period as an additive or multiplicative effect did not increase the model fit indicating that the same quantitative relationship held between rainfall and rate of increase between the two Periods (Table 1). Positive rates of increase occurred when the rainfall over the April–October period was generally above 200 mm. The average April–October rainfall for the Historic period was significantly higher than for the Recent period (222.5 mm vs 161.5 mm;  $F_{1,24} = 5.206, P = 0.032$ ).

Faster rates of population decrease were associated with higher autumn trap success ( $F_{1,21} = 94.1, P < 0.001$ ; Fig. 4). Adding Period as a multiplicative effect did not



**Fig. 2** Trap success (ATS) of mice at Walpeup from 1983 to 2020. The time series is divided into ‘conventional agriculture’ Historic Period (1983–2002, circles) and ‘conservation agriculture’ Recent Period (2012–2020, triangles)



**Fig. 3** Monthly rate of population change ( $r$ ) from crop season (spring) to non-crop season (autumn) plotted against the immediately previous winter (April–October) rainfall. Historic data shown in orange circles, Recent data in blue

**Table 1** Summary of Model A for comparative analysis of mouse rates of increase as a function of winter rainfall (April–October) and Period (Historic vs Recent) over the spring population low to autumn population high

Model	DF	AICc	$\Delta$ AICc
<b>RAINFALL</b>	3	<b>- 7.28</b>	<b>0</b>
RAINFALL + PERIOD	4	- 5.31	1.97
RAINFALL $\times$ PERIOD	5	- 3.92	3.36

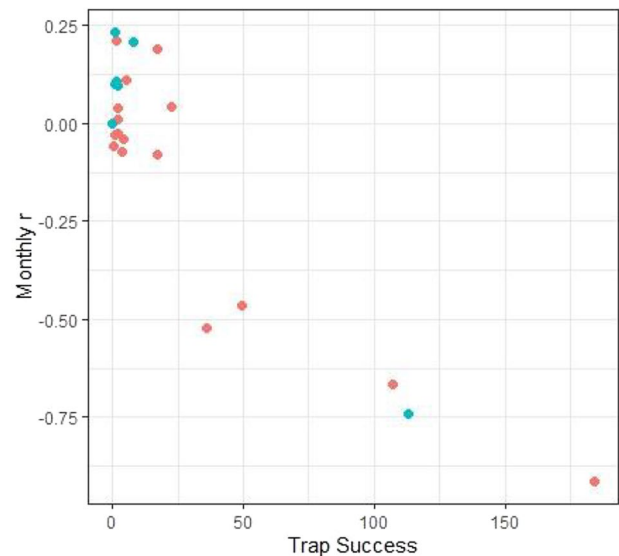
The most parsimonious model included Rainfall only (bold)

increase the model fit ( $\Delta$ AICc < 2.0) indicating that the same quantitative relationship held between trap success at the beginning of the decrease and the rate of decrease between the two Periods (Table 2).

The overall irruptive nature of the Walpeup populations was consistent between the Historic and Recent Periods. These results support Prediction H1 that the underlying population dynamics of the mouse populations at the research site have not changed over the two data collection Periods.

### Comparative use of crop-margin habitats by mice over the cropping cycle

During the Historic Period (1983–2002), by far the best model to explain variation in trap success was one that included the interaction effect of Habitat and Season on top of the fixed effects themselves (Model C, Table 3, Historic data). Trap success was significantly lower in Paddocks



**Fig. 4** Monthly rate of population change ( $r$ ) from the non-crop season (autumn) to the crop season (spring) plotted against trap success (ATS) in the non-crop season. Historic data shown in orange, Recent data in blue

**Table 2** Summary of Model B for comparative analysis of mouse rates of decrease as a function of trap success in autumn and Period (Historic vs Recent)

Model	DF	AIC	$\Delta$ AIC
<b>TRAP SUCCESS</b>	<b>3</b>	<b>- 22.6</b>	<b>0</b>
TRAP SUCCESS $\times$ PERIOD	5	- 22.4	0.2
TRAP SUCCESS + PERIOD	4	- 21.4	1.2

The most parsimonious model included trap success only (bold)

during the Non-Crop Season (HABITAT  $\times$  SEASON parameter estimate confidence intervals do not overlap zero, Supplementary Table 1).

During the Crop Season, trap success was higher in the Paddocks compared to Margins, but during the post-harvest Non-Crop Season, trap success significantly increased in Margins (Fig. 5, top panels). This result supports Prediction H2. Trap success was a little higher overall in the Non-Crop Season as this is following the beginning of breeding and during the population's increase phase (Supplementary Table 3).

In the Recent Period (2012–2020), the inclusion of the interaction effect of HABITAT  $\times$  SEASON was indistinguishable from the model with the fixed effect of HABITAT only ( $\Delta$ AICc = 0.5, Table 3, Model C, Recent data). Trap success was a little higher (but not significantly so: Supplementary Table 2: CI's overlapping zero) overall in Paddocks and this is maintained throughout the Crop and Non-Crop

**Table 3** Summary of Models C and D for comparative analysis of mouse abundance between Margin and Crop Habitats for the Historic Period (1983–2002), Recent Period (2012–2020), and for all data combined

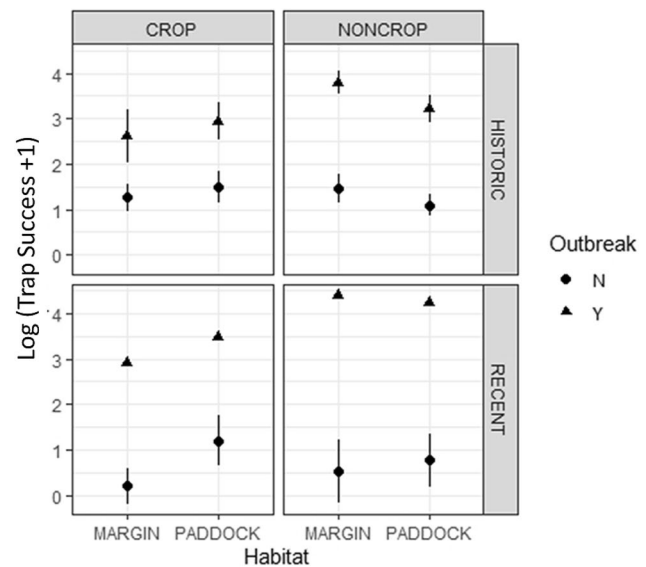
Model	DF	AICc	$\Delta$ AICc
<i>Model C: Historic data</i>			
<b>HABITAT <math>\times</math> SEASON</b>	<b>6</b>	<b>453.2</b>	<b>0</b>
SEASON	4	464.6	11.4
HABITAT + SEASON	6	464.7	11.5
<i>Intercept</i>	3	470.2	17.0
HABITAT	4	470.4	17.2
<i>Model C: Recent data</i>			
<b>HABITAT <math>\times</math> SEASON</b>	<b>6</b>	<b>95.9</b>	<b>0</b>
<b>HABITAT</b>	<b>4</b>	<b>96.4</b>	<b>0.5</b>
HABITAT + SEASON	5	98.3	2.4
<i>intercept</i>	3	100.3	4.4
SEASON	4	102.2	6.3
<i>Model D: All data</i>			
<b>HABITAT <math>\times</math> SEASON + HABITAT <math>\times</math> PERIOD</b>	<b>8</b>	<b>642.95</b>	<b>0</b>
HABITAT $\times$ SEASON	6	648.73	5.78
PERIOD $\times$ SEASON + HABITAT $\times$ SEASON	8	649.7	6.75
HABITAT $\times$ SEASON + HABITAT $\times$ PERIOD + SEASON $\times$ PERIOD	9	651.54	8.59
HABITAT $\times$ SEASON $\times$ PERIOD	10	652.52	9.57
HABITAT + SEASON + PERIOD	6	663.28	20.33
SEASON + HABITAT	5	664.11	21.16
HABITAT + PERIOD	5	664.39	21.44
HABITAT	4	665.41	22.46
HABITAT $\times$ PERIOD	6	665.8	22.85
PERIOD $\times$ SEASON + PERIOD $\times$ HABITAT	8	666.45	23.50
SEASON + PERIOD	5	668.27	25.32
SEASON	4	669.1	26.15
PERIOD	4	669.2	26.25
SEASON $\times$ PERIOD	6	670.01	27.06
<i>Intercept</i>	3	670.21	27.26

The most parsimonious models in bold

Seasons (Fig. 5, bottom panels). Importantly, trap success does not decrease in Paddocks during the Non-Crop season post-harvest supporting Prediction H3.

Using all data and testing for a three way interaction effect we found the most parsimonious model included the interaction effects of HABITAT  $\times$  SEASON and HABITAT  $\times$  PERIOD (Table 3, Model D, Supplementary Table 3: CI's overlapping zero) but not the SEASON  $\times$  HABITAT  $\times$  PERIOD effect ( $\Delta$ AICc = 9.6). Data and model predictions for the most parsimonious subset of Model D are presented in Supplementary Fig. 1.

Over time, the relative trap success of mice on Margins has diminished during the Non-Crop Season (Fig. 5).



**Fig. 5** Mean adjusted trap success (log scale  $\pm$  95% CI) in Paddock and Margin habitats during the Historic period (top panels) and Recent period (bottom panels), and during the Crop season (left panels) and Non-Crop season (right panels). Outbreak years and non-outbreak years separated. There was only 1 outbreak year in the recent data period (No CI's)

Furthermore, trap success does not decrease in Paddocks during the Non-Crop Season post-harvest. Over both Periods of data, Margins were used more during the Non-Crop Season but trap success along margins was generally lower in the Recent Period than it was in the Historic Period. There was no significant PERIOD  $\times$  SEASON interaction meaning that trap success was higher in the Non-Crop Season than the Crop Season over both Periods as populations increased from the spring low (Crop Season) through the late-summer-autumn (Non-Crop Season) high. This was consistent between Periods and probably contributed to there being no significant three-way interaction as postulated by Prediction H4.

## Discussion

Our analysis of the historical and recent data show that since the introduction of CA, mice have changed their habitat use in Australian grain cropping landscapes although regional drivers of population increases and decreases remain the same. We found a difference in the way mice use margin habitats during the non-crop season between the historical (1983–2002) and recent (2012–2020) trapping periods. Mice now remain resident in paddocks both during crop and non-crop phases of the cropping cycle. Mice still use margin habitats (fence lines and road verges etc.) but at lower

abundance than prior to the introduction of Conservation Agriculture.

It is likely that this change is due to less soil disturbance associated with CA practices meaning that mouse burrows remain intact within paddocks following harvest. During ‘conventional’ farming, mouse burrows were routinely disturbed as farm machines were used to control weeds, prepare seed beds and plant crops (Pankhurst et al. 1995). It is not surprising that the unploughed margin habitats were invaded following harvest.

The recent more environmentally sensitive CA practices are providing far more benign conditions for mice. CA includes more than just zero- or no-till (Kirkegaard et al. 2014; Knowler and Bradshaw 2007); it has led to a change in crop rotation practices. Historically crop rotations included lengthy stubble and fallow phases and grazing to remove residual grain and weeds was a key component of stubble management. Now paddocks have crop in them most years, standing stubble, and no physical disturbance associated with ploughing meaning the crop area provides a year-round safe environment for mice reducing any impetus for a population to move. Singleton and Brown (1999) suggested that these conditions associated with CA adoption in Australia could result in higher frequencies of population eruptions. Longer term monitoring is required to determine if this will be the case.

Approximately 80% of Australian farmers now grow winter cereals using CA principles (Llewellyn et al. 2012). Drought is a significant and regular characteristic of Australian agriculture, and many land management strategies are targeted around minimising the risks associated with low and irregular rainfall (Kirkegaard et al. 2014). CA acts to increase water efficiency in several ways; reducing evaporation by maintaining cover and reducing tillage, and increasing infiltration by improving surface soil structure and by providing preferential flow via standing stubble (Bellotti and Rochecouste 2014). A highly significant consequence of CA is the value added from earlier sowing, thereby reducing moisture loss to weeds and/or evaporation. Globally, CA is now practised on over 125 M ha, covering approximately 10% of the global arable land surface. This compares to only 45 M ha in 2004 (Friedrich et al. 2012). It would not be unexpected for other agricultural rodent pests around the world to have also modified their habitat use necessitating changes in management practises.

## Implications for management

Brown et al. (2004; 2010) recommended the management of margin habitats by slashing or spraying weeds to reduce cover and increase predation risk in refuge habitats (‘source’ habitats) which may lead to a reduction in mouse abundance and damage to crops. This recommendation may no longer

be relevant. The benefits of conservation agriculture for the farming system makes it unlikely farmers will consider ploughing their fields to manage mice, however, the benefits of ‘strategic tillage’ for the management of herbicide resistant weeds, aspects of soil health and to manage soil structure (Kirkegaard et al. 2014) may also have benefits for destroying long-lived mouse burrows.

The application of broad scale rodenticides has been a key management tool for grain-growers for many years (Brown et al. 2002, 1997; Mutze 1993; Mutze and Sinclair 2004; Saunders 1983; Twigg et al. 1991), but questions remain about the best time and location for application to achieve greatest benefit to minimise crop damage and therefore economic loss. Perimeter baiting has been restricted by product-label conditions (bait should not be placed within 50 m of wildlife habitats along crop margins) but our analysis demonstrates that under CA management mice do not preferentially use these margin habitats. In southern cropping regions of Australia, most damage to crops occurs at sowing when mouse abundance is high at the end of the breeding season (Brown et al. 2007). Rainfall remains the best predictor of outbreaks via its effect on food availability and population rate of increase, and can be used to anticipate impending plagues and levels of management required (Davis et al. 2003; Kenney et al. 2003; Pech et al. 1999). The best option for bait application remains to bait at sowing or shortly before to protect crops at a critical time. Cereal crops (particularly wheat) can compensate for most mouse damage, particularly if the damage occurs early in the crop growth (Brown 2005; Brown et al. 2007).

Other options for managing mouse populations and potentially reducing mouse damage are to reduce food and cover resources. Food and water are important components that enable mouse populations to thrive (Brown et al. 2008, 2020). Reducing food resources could be achieved by minimising the amount of grain left on the ground after harvest. This could be achieved by improvements to harvesting machinery efficiency or using ‘seed destroyer/destroyer’ technologies (Walsh et al. 2012), which are being developed to overcome herbicide resistant weeds. Other approaches to reduce amount of spilt grain is to graze the crop stubble post-harvest, but many farmers are moving out of live-stock grazing. A light tillage post-harvest could bury some remaining food sources making it harder for mice to find.

Increasing predation risk by reducing cover is another option available to grain growers (Jacob 2008). Reducing cover could be achieved by prickle chain, small disk chain, speed tilling, or rolling stubble, but this depends on the cropping system and the equipment available to the farmer. Although very few studies show that avian predation reduces small mammal populations (Labuschagne et al. 2016), avian predator numbers do increase in response to increased mouse abundance (Arthur et al.



2004; Sinclair et al. 1990) and mouse behaviour changes in relation to available cover to minimise predation risk (Arthur and Pech 2003; Arthur et al. 2003b; Ylonen et al. 2002). It is likely that the risk of predation leads to reduced damage, rather than the actual ‘predation’ itself. Predation risk for mice in the grain growing systems requires more research.

The analysis in this paper shows that mice no longer primarily use margin habitats as refuge following harvest but instead are resident in paddocks throughout the year. Research is required to make current control strategies more effective; understanding mouse population dynamics in CA systems will be critical for the development of highly targeted control strategies.

### Authors’ contributions

WR, PB and SH designed this analysis. Historic data collected by GS and the CSIRO Rodent Team v1. Recent data collection designed by PB, SH, LH, and collected by all authors ex GS (CSIRO Rodent Team v2). WR analysed the data. WR and PB wrote the first draft, all authors contributed to the final manuscript.

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**Data availability** Data are held by the Commonwealth Science and Industry Research Organisation (CSIRO), Australia.

**Code availability** Available from author WR on request.

### Declarations

**Conflicts of interest** The authors declare that they have no conflict of interest.

**Ethics approval** This work has been approved by the CSIRO Wildlife and Large Animal Ethics Committee (most recent approval: 2018–33 ‘Mouse monitoring and surveillance’) and adheres to the 8<sup>th</sup> Edition of the Australian Code and Use of Animals for Scientific Purposes. This article does not contain any studies with human participants performed by any of the authors.

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