

# Spatial and temporal drivers of small mammal distributions in a semi-arid environment: The role of rainfall, vegetation and life-history

LUKE T. KELLY,<sup>1\*</sup> RAY DAYMAN,<sup>3</sup> DALE G. NIMMO,<sup>1</sup> MICHAEL F. CLARKE<sup>2</sup> AND ANDREW F. BENNETT<sup>1</sup>

<sup>1</sup>*Landscape Ecology Research Group, School of Life and Environmental Sciences, Deakin University, Burwood,* <sup>2</sup>*Department of Zoology, La Trobe University, Bundoora, Victoria,* and <sup>3</sup>*Office of Environment and Heritage, National Parks and Wildlife Service, Lower Darling Area, New South Wales, Australia*

**Abstract** A key task in ecology is to understand the drivers of animal distributions. In arid and semi-arid environments, this is challenging because animal populations show considerable spatial and temporal variation. An effective approach in such systems is to examine both broad-scale and long-term data. We used this approach to investigate the distribution of small mammal species in semi-arid ‘mallee’ vegetation in south-eastern Australia. First, we examined broad-scale data collected at 280 sites across the Murray Mallee region. We used generalized additive mixed models (GAMMs) to examine four hypotheses concerning factors that influence the distribution of individual mammal species at this scale: vegetation structure, floristic diversity, topography and recent rainfall. Second, we used long-term data from a single conservation reserve (surveyed from 1997 to 2012) to examine small mammal responses to rainfall over a period spanning a broad range of climatic conditions, including record high rainfall in 2011. Small mammal distributions were strongly associated with vegetation structure and rainfall patterns, but the relative importance of these drivers was species-specific. The distribution of the mallee ningau *Ningau yvonneae*, for example, was largely determined by the cover of hummock grass; whereas the occurrence of the western pygmy possum *Cercartetus concinnus* was most strongly associated with above-average rainfall. Further, the combination of both broad-scale and long-term data provided valuable insights. Bolam’s mouse *Pseudomys bolami* was uncommon during the broad-scale survey, but long-term surveys showed that it responds positively to above-average rainfall. Conceptual models developed for small mammals in temperate and central arid Australia, respectively, were not, on their own, adequate to account for the distributional patterns of species in this semi-arid ecosystem. Species-specific variation in the relative importance of different drivers was more effectively explained by qualitative differences in life-history attributes among species.

**Key words:** arid, habitat, landscape, mammal, species distribution model.

## INTRODUCTION

Understanding and identifying the drivers of animal distributions is a major task in ecology (Brown 1995). A key challenge relates to the small spatial and short temporal scales over which ecological studies often are conducted, compared with the large scales over which many ecological processes operate (Meserve *et al.* 2003). In arid and semi-arid environments, for example, marked variation in rainfall may occur between months, years and decades (Holmgren *et al.* 2006; Morton *et al.* 2011); and animal populations

may show considerable spatial variation in distribution and abundance (Dickman *et al.* 2011; Ojeda *et al.* 2011). An effective means of disentangling the drivers of animal distributions is to use a combined approach that integrates both broad-scale (spatial) and long-term (temporal) data (Meserve *et al.* 2003; Haythornthwaite & Dickman 2006).

Studies of small mammals have provided valuable insights into the determinants of the distribution and abundance of animal species in space and time (Kelt 2011). In several well-studied systems, large-scale data have been used to develop and test conceptual models that synthesize the primary factors that influence small mammal distributions. In South America, Meserve *et al.* (2003) used broad-scale and long-term data to investigate shifting ‘top-down’ and ‘bottom-up’ controls on species distributions. In North America, Brown

\*Corresponding author. Present address: School of Botany, The University of Melbourne, Parkville, Vic. 3010, Australia (Email: ltkelly@unimelb.edu.au).

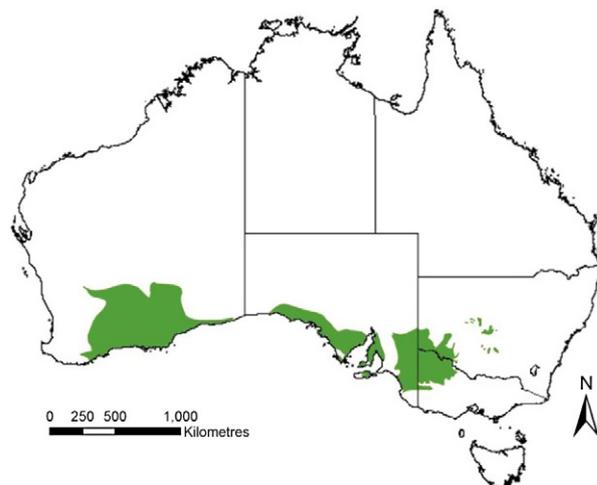
Accepted for publication December 2012.

and Ernest (2002) used long-term data to investigate a model of water resource regulation of desert rodent populations. In Australia, long-term data have contributed to the development of conceptual models that explain patterns of small mammal distribution in both the central arid zone (Letnic & Dickman 2010) and temperate coastal areas (Fox 1996).

In arid central Australia, the distribution and abundance of small mammals typically correlate poorly with vegetation structure (Letnic *et al.* 2004). Rather, rainfall appears to be a primary determinant of the structure of small mammal assemblages (Southgate & Masters 1996; Dickman *et al.* 1999). Letnic *et al.* (2004) developed a state-and-transition model that highlights multiple states in the composition of arid-zone assemblages of small mammals, with different states developing in response to specific environmental conditions. The key element of this model is the strong influence of rainfall-driven changes in food resources on small mammal assemblages (Letnic & Dickman 2010).

In temperate environments in Australia, patterns of small mammal distribution are strongly correlated with vegetation structure and composition (Holland & Bennett 2007; Monamy & Fox 2010). Fox (1982) developed a model of animal succession to describe changes in a small mammal assemblage following fire in eastern Australia. The 'habitat accommodation model' proposed that small mammal species enter the mammalian succession when vegetation structure becomes suitable for them. As the structure of the vegetation changes and becomes less suitable, a species will be excluded from the succession, or become reduced in abundance, by competition (Fox *et al.* 2003; Monamy & Fox 2010).

'Mallee' vegetation occurs primarily in semi-arid southern Australia where it forms an intermediate zone between temperate environments of the south and arid environments of the interior (Fig. 1; Bennett *et al.* 1989). Mallee ecosystems are characterized by small multi-stemmed eucalypts, and contain a distinct small mammal assemblage, which includes dasyurids (insectivorous marsupials), burramyids (nectarivorous pygmy possums) and murids (omnivorous rodents) (Bennett *et al.* 2006). Several studies have examined the distribution of small mammals in mallee vegetation at local scales (Bos *et al.* 2002; Bos & Carthew 2003), documented their responses to fire history (Kelly *et al.* 2011, 2012), and described biogeographic patterns (Menkhorst & Bennett 1990; Bennett *et al.* 2006). However, there is limited knowledge of the explanatory power, predictability and relative influence of potential drivers of species distributions at large spatial and temporal scales. There is a need to synthesize the drivers of this assemblage to advance our understanding of small mammal distribution, ecology and conservation.



**Fig. 1.** Mallee shrublands and woodlands of semi-arid Australia (shaded areas). Modified from Noble (1984).

Here, we investigated the factors that influence the distribution of small mammals in semi-arid mallee ecosystems using complementary broad-scale and long-term data sets. First, we examined broad-scale data collected at 280 sites distributed across a large geographic area, the Murray Mallee Region (104 000 km<sup>2</sup>). At this scale, we used regression models to examine four key features of the environment that could determine the distribution of individual mammal species: these were vegetation structure, floristic diversity and flowering, topography and local rainfall. Second, we examined long-term data from one conservation reserve within the region: Tarawi Nature Reserve (NR) (surveyed from 1997 to 2012). At this scale, we documented small mammal responses to rainfall over periods spanning above- and below-average conditions; including a year of record high rainfall in 2011. Finally, we compared the drivers of small mammal distributions in semi-arid Australia with those identified from arid and temperate systems. Based on the habitat accommodation model, we expected that vegetation structure would be the primary determinant of small mammal distributions. Alternatively, based on the resource-pulse model, we expected that rainfall would be the primary determinant of small mammal distributions.

## METHODS

### Study area

The Murray Mallee region (33°56'39"S, 141°44'30"E) encompasses several large reserves managed for nature conservation in Victoria, South Australia and New South Wales. The landscape is of low elevation ( $\leq 100$  m above sea level),

with moderate topographic variation provided by undulating dune and swale systems. Sandy flats are characterized by an overstorey of *Eucalyptus dumosa* and *E. socialis*, and an understorey including the hummock grass *Triodia scariosa* and the shrubs *Acacia rigens* and *Beyeria opaca*. Sand dunes are characterized by the presence of *Eucalyptus costata* and the conifer *Callitris verrucosa*. On swales with heavier soils, common overstorey species are *Eucalyptus oleosa* and *E. gracilis*, over low perennial shrubs such as *Maireana* spp., *Atriplex* spp. and *Zygophyllum* spp.

The climate of the region is semi-arid; mean annual rainfall ranges from ~250 mm in the north to 300 mm in the south. Rainfall typically is non-seasonal and interannual rainfall variability is high. Mean daily maximum temperatures in summer range from 30°C to 33°C and temperatures >40°C are common. Winters are mild, with mean daily maximum temperature ranging from 15°C to 18°C across the region (Australian Bureau of Meteorology: <http://www.bom.gov.au/>).

In 2010 and 2011, large areas of the Murray Mallee region experienced very high rainfall. Tarawi NR received its highest annual rainfall on record in 2011 (668 mm, compared with median annual rainfall of 245 mm). This provided an opportunity to examine the influence of rainfall-driven resource pulses on small mammal populations in semi-arid mallee ecosystems.

### Sources of mammal data

The broad-scale data form one component of an extensive project examining the biodiversity of the study area: the Mallee Fire and Biodiversity Project. The 280 sites included in this investigation were grouped into clusters representing 28 study landscapes, each a circular area of 12.56 km<sup>2</sup>. Ten survey sites were established in each landscape (see Kelly *et al.* 2012 for further details).

Long-term data from Tarawi NR (eight sites) were collected by the National Parks and Wildlife Service, New South Wales. Sites representative of the 34 500-ha reserve were selected as part of a long-term monitoring project. Data analysed in the present study were from sites located in mallee shrublands and woodlands.

### Small mammal surveys

At each broad-scale survey site, we established a line of pitfall traps comprising 10 20-L plastic buckets, spaced 5 m apart, connected by a continuous 300-mm-high flywire drift-fence. Surveys were conducted at each of the 280 sites four times: starting dates were October–November 2006 (spring), January–February 2007 (summer), October–November 2007 (spring) and January–February 2008 (summer). Each survey period consisted of five consecutive nights of trapping, with traps checked daily. Elliot aluminium box traps (33 × 10 × 10 cm) were used to complement pitfall trapping in spring survey periods, but not in summer (to ensure the welfare of animals during high summer temperatures). In spring surveys, five Elliot traps were placed adjacent to the pitfall line at each site. The

species of captured animal was recorded, and hair clipping was used to mark individuals and identify recaptures during each survey period. In total, we completed 56 000 pitfall trap nights and 14 000 Elliot trap nights. Prior to statistical analysis, we grouped the data from the broad-scale surveys to represent two time periods: spring/summer 2006/2007 and spring/summer 2007/2008. This grouping, based on the warm-season breeding period of several species, enabled a clearer examination of the effects of rainfall on small mammals at large spatial scales.

Long-term surveys followed a similar protocol (i.e. pitfall-trapping over consecutive days, hair clipping to mark animals). At Tarawi NR, small mammal surveys were conducted at eight sites. Six sites were surveyed on 14 occasions between 1997 and 2012: November 1997, January 1998, February 1998, March 1998, February 2000, November 2000, February 2001, December 2001, November 2002, March 2004, November 2004, January 2005, December 2011 and February 2012. Two additional sites were surveyed on the last seven occasions only, and a survey completed in March 2012 included four sites only. Between 80 and 100 pitfall trap nights were completed at each site in each survey period (a total of 9900 trap nights).

### Vegetation structure, floristic diversity and topography

We measured attributes of vegetation structure and floristic diversity at each broad-scale site, assessed once (August–September 2007). Ground cover (categorized as litter, bare ground, logs, perennial plants and herbs), and the presence of *Triodia* hummocks and shrubs, were recorded at 1 m intervals along a 50-m transect at each site. Using a measuring pole, hummock grass and shrub records were grouped into four above-ground intervals: <0.5 m, 0.5–1 m, 1–2 m and >2 m, at each interval along the 50-m transect. Structural attributes of mallee eucalypts encountered on the transect were also measured, including stem diameter and the presence of stems with hollows. Average canopy height was estimated to the nearest metre for the dominant eucalypt cohort at each site. Floristic surveys were undertaken in a 10 × 50-m belt transect at each site. All perennial plant species present were recorded. Perennial and ephemeral plant cover was relatively consistent throughout the course of this study. Land position was categorized as a dune, flat or swale, based on inspection of the soil and local topography. The presence or absence of eucalypt flowering was assessed at each site during each faunal survey period, in a 10 × 20-m belt transect.

### Rainfall data

The recent rainfall history of all long-term and broad-scale sites was represented by the amount of rainfall (mm) summed over a 12-month period. Observed monthly rainfall data were obtained from the closest weather station (Australian Bureau of Meteorology: <http://www.bom.gov.au/>) to each cluster of sites ( $n = 9$ , mean distance to closest station = 25 km (range 4–50 km)). We examined species

responses to rainfall values at time lags of 3, 6, 9 and 12 months, as we expected responses to rainfall-driven changes in resources to be time delayed. For broad-scale data, time lags were calculated as of Nov 2006 and Nov 2007 (the mid-point of the first survey during each grouped survey period). For long-term data, time lags were calculated as of each individual survey period.

### Analyses of broad-scale data

We used generalized additive mixed models (GAMMs: Wood 2006) to investigate small mammal responses to predictor variables. GAMMs provide a flexible framework with which to build species distribution models: first, predictors can be fitted as either non-linear or linear terms, and second, sources of correlation structure in the data can be included in models as random effects. For analyses of the broad-scale data, the response variable was the detected presence or absence of a species at a site for each grouped survey period. GAMMs were implemented with a logit link function and binomial errors (Wood 2006). Continuous predictor variables were entered as non-linear smoothed terms. Categorical variables were entered as linear terms. The study landscape was included as a random effect to account for expected spatial correlation structure in the data within clusters of sites. Site was entered as a random effect to account for possible temporal correlation of sites surveyed repeatedly.

To reduce the number of variables in the model set for each species, we first examined univariate GAMMs of each species with each explanatory variable (see Appendix S1). Exploratory analyses indicated that several variables representing vegetation structure were important determinants of species distribution. Consequently, we divided this category into measures relating to three strata of vegetation: low, mid and high. We then selected for further analysis for each species, the variable with the best model fit for a given hypothesis. Thus, each species model set included six variables: three representing vegetation structure (low, mid and high strata), and one representing each of floristic diversity and flowering, topography and rainfall. All variables in each species model set had pair-wise Spearman rank correlation coefficients of less than  $<0.6$ .

For each species, we ran models of all possible subsets of the six explanatory variables. Alternative models were ranked using Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ).  $AIC_c$  ranks models according to the weight of evidence in favour of each, based on their fit to the data and the number of parameters in the model (Burnham & Anderson 2002). For each model, the  $AIC_c$  difference ( $\Delta_i$ ) and the Akaike weight ( $w_i$ ) were also calculated. The  $AIC_c$  difference is the difference between the  $AIC_c$  value for a particular model and that for the 'best' model (i.e. the model with the lowest  $AIC_c$  value). The Akaike weights of a model set sum to 1.0 and indicate the weight of evidence in favour of each model, out of the set of models considered (Burnham & Anderson 2002). Burnham and Anderson (2002) suggest that models having  $\Delta_i$  values  $\leq 2$  have substantial support.

For all models with  $\Delta_i$  values  $\leq 2$ , we assessed the fit and predictive accuracy of the model. Model fit was evaluated

using the percentage of null deviance explained (% Dev) (Zuur *et al.* 2009). The ability of each model to discriminate between species presence and absence was assessed by using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Pearce & Ferrier 2000). We calculated AUC values using a cross validation procedure. Landscape clusters were randomly divided into seven 'folds' (groups). A GAMM was built using data from six folds (240 sites) and then was used to predict to sites from the seventh fold (40 sites). The process was repeated until predictions had been obtained for each of the seven data folds by using data separate from the model-building process. This procedure was repeated three times for each model. We report the mean and standard error of AUC values. Models with AUC values of  $<0.7$ ,  $0.7-0.9$  and  $>0.9$  were interpreted as offering poor, useful and very good discrimination respectively (Pearce & Ferrier 2000).

### Analyses of long-term data

For the long-term data, we modelled the response variable as the capture rate of each species at a given site, for a given survey period. Capture rate = total captures of a species/total trap nights. We focused on abundance (rather than occurrence) at this scale for two reasons: first, exploration of the data showed that some species were present during most surveys; and second, to allow for a clear comparison with the results of other long-term studies from the arid zone. GAMMs were implemented with a logit link function and binomial errors (Wood 2006). Univariate models were run for each species in relation to summed rainfall values, with the latter entered as non-linear smoothed terms. Site was entered as a random effect to account for the expected temporal correlation of sites measured repeatedly. We present univariate models of the best-fitting regression model for each species.

All statistical analyses were undertaken in the R statistical package version 2.15.0 (R Development Core Team 2012). GAMMs for the broad-scale data were run in the extension package *gamm4* version 0.1-6 and GAMMs for the long-term data were run in the extension package *mgcv* version 1.7-20 (Wood 2006). Percentage deviance explained and cross validation AUC values were calculated using a modified version of script from Elith *et al.* (2008).

## RESULTS

### Regression models for broad-scale data

Broad-scale faunal surveys resulted in 1265 captures of seven mammal species. The small mammal assemblage was composed of two species of dasyurid marsupials, the mallee ningau *Ningau yvonneae* (detected at 147 sites) and common dunnart *Sminthopsis murina* (153 sites); two burramyids, the western pygmy possum *Cercartetus concinnus* (85 sites) and little pygmy possum *Cercartetus lepidus* (15 sites); and three rodents, Bolam's mouse *Pseudomys bolami*

**Table 1.** Results of generalized additive mixed models describing the relationship between small mammals and candidate predictor variables at broad scales

Species	Model	<i>K</i>	AIC <sub>c</sub>	Δ <sub>i</sub>	W <sub>i</sub>	% Dev	AUC ± SE
<i>Cercartetus concinnus</i>	Rainfall <sup>1</sup> + Vegetation structure <sup>2</sup>	7	374.06	0.00	0.21	19	0.79 ± 0.04
	Rainfall <sup>1</sup> + Vegetation structure <sup>2,3</sup>	9	374.33	0.27	0.19	20	0.80 ± 0.04
	Floristic diversity <sup>4</sup> + Vegetation structure <sup>2</sup> + Rainfall <sup>1</sup>	8	375.57	1.50	0.10	20	0.79 ± 0.04
<i>Mus musculus</i>	Floristic diversity <sup>4</sup> + Vegetation structure <sup>2,3</sup> + Rainfall <sup>1</sup>	10	375.88	1.82	0.09	20	0.79 ± 0.04
	Rainfall <sup>1</sup> + Vegetation structure <sup>3</sup>	8	459.46	0.00	0.23	17	0.78 ± 0.03
	Rainfall <sup>1</sup> + Vegetation structure <sup>3</sup>	7	460.16	0.69	0.16	17	0.78 ± 0.02
<i>Ningau yvonneae</i>	Floristic diversity <sup>5</sup> + Rainfall <sup>1</sup> + Topography + Vegetation <sup>3</sup> structure <sup>2</sup>	10	460.30	0.84	0.15	18	0.77 ± 0.03
	Rainfall <sup>1</sup> + Topography + Vegetation <sup>3</sup>	9	460.90	1.44	0.11	18	0.78 ± 0.04
	Vegetation structure <sup>2,3,6</sup>	9	568.67	0.00	0.21	25	0.79 ± 0.03
	Vegetation structure <sup>2,3</sup>	7	569.17	0.50	0.17	23	0.79 ± 0.04
<i>Sminthopsis murina</i>	Vegetation structure <sup>2,3,6</sup> + Topography	11	570.26	1.59	0.10	26	0.79 ± 0.03
	Floristic diversity <sup>5</sup> + Vegetation structure <sup>2,3,6</sup>	10	570.33	1.66	0.09	25	0.79 ± 0.03
	Floristic diversity <sup>8</sup> + Rainfall <sup>1</sup> + Vegetation structure <sup>7</sup>	9	666.62	0.00	0.33	5	0.65 ± 0.03
	Rainfall <sup>1</sup> + Vegetation structure <sup>7</sup>	7	668.53	1.92	0.13	4	0.64 ± 0.03

Represented by variable(s): <sup>1</sup>6-month lag, <sup>2</sup>Hummock Grass, <sup>3</sup>Canopy Height, <sup>4</sup>Eucalypt Flowering, <sup>5</sup>Herbs, <sup>6</sup>Bare ground, <sup>7</sup>Hollows, <sup>8</sup>Chenopod. See Appendix S1 for descriptions of each variable. *K* = number of model parameters. AIC<sub>c</sub> = Akaike's Information Criterion corrected for small sample size. Δ<sub>i</sub> = delta AIC. W<sub>i</sub> = Akaike weight of model. % Dev = percentage deviance explained. AUC = area under the curve of a ROC analysis, calculated using cross validation.

(18 sites), Mitchell's hopping mouse *Notomys mitchelli* (6 sites) and the house mouse *Mus musculus* (80 sites). We undertook statistical analyses on species captured at 20 or more sites (those most suitable for regression analyses).

Regression modelling of the occurrence of *C. concinnus* resulted in four models with substantial support (i.e. Δ<sub>i</sub> < 2) (Table 1). Model fit was moderate (% Dev = 19–20%) and with AUC values ≥ 0.79 the models offer useful discrimination between the presence and absence of *C. concinnus*. Summed Akaike weights (Σw<sub>i</sub>) of each candidate predictor indicated that variables representing rainfall (1.0) and vegetation structure (0.86) were influential (Fig. 2a–d). The probability of occurrence of *C. concinnus* was strongly associated with 12-month rainfall (at a 6-month time lag) (Fig. 3a). *Cercartetus concinnus* was also associated with increasing canopy height and the cover of hummock grass (Table 1). The presence of flowering *Eucalyptus* spp. was not a strong influence on the occurrence of *C. concinnus* after considering rainfall (Σw<sub>i</sub> = 0.32).

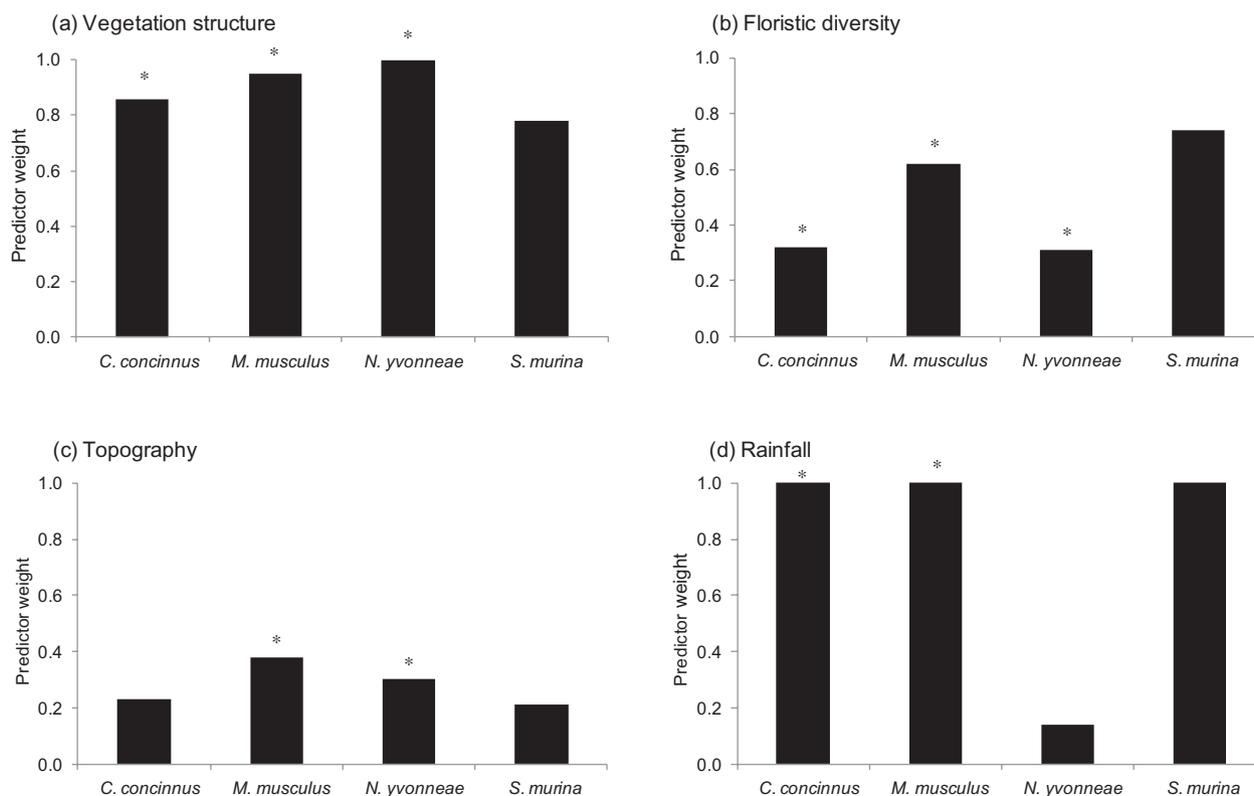
For *M. musculus*, four models had substantial support (Table 1), and AUC values of 0.77–0.78 indicated useful model discrimination. Variables representing three hypotheses were important influences, based on summed Akaike weights: rainfall (1.0), vegetation structure (0.95) and floristic composition (0.62) (Fig. 2a–d). *Mus musculus* was positively associated with 12-month rainfall at a 6-month time lag (Fig. 3b). The probability of occurrence of *M. musculus* increased at sites with low canopy cover and where grasses and herbs were present (Table 1).

Four models for *N. yvonneae* had substantial support (Table 1): model fit was moderate (% Dev = 23–25%) and AUC values of 0.79 indicated useful model discrimination. Variables representing vegetation structure were clearly the most influential of the candidate predictors (Fig. 2a–d). *Ningau yvonneae* was most strongly associated with sites having high cover of hummock grass (Fig. 3c). Rainfall and floristic diversity had little influence on its occurrence.

Regression modelling for *S. murina* resulted in two models with Δ<sub>i</sub> < 2 (Table 1). However, these had poor model fit (% Dev ≤ 5) and offered little discrimination between the species presence and absence at sites (AUC < 0.70). We interpreted these results as offering little support that the candidate predictors are key determinants of the distribution of *S. murina* at large spatial scales.

### Regression models for long-term data

Surveys at Tarawi NR resulted in 935 captures of eight mammal species. The small mammal assemblage was composed of *N. yvonneae* (638 captures at 15 surveys), *S. murina* (33 captures at 10 surveys); the fat-tailed dunnart *Sminthopsis crassicaudata* (7 captures at 2 surveys), *C. concinnus* (2 captures at 1 survey), *M. musculus* (170 captures at 6 surveys), *P. bolami* (83 captures at 11 surveys) and the desert mouse *Pseudomys desertor* (2 captures at 2 surveys). We undertook statistical analyses on species with more than 20 capture records.



**Fig. 2.** Relative importance of predictor variables representing four hypotheses determining the broad-scale distribution of small mammals in semi-arid mallee vegetation: vegetation structure, floristic diversity, topography and rainfall. Columns are summed Akaike weights ( $\Sigma w_i$ ) of the best-fitting variable representing each hypothesis, for each species model set. An asterisk is shown for variables that occur in the species best model set ( $\Delta_i < 2$ ) and for which that model shows evidence of useful discrimination ability (area under the curve  $\geq 0.70$ ).

Summed rainfall values at Tarawi NR were occasionally higher than those for calendar years. In March 2012, for example, the amount of rainfall summed over a 12-month period (at a 12-month time lag) reached 940 mm. Rainfall was a strong influence on the variation in captures through time for two of the four most common species at Tarawi NR (Fig. 4a–d). Univariate regression models showed that two rodents, *P. bolami* and *M. musculus*, were positively influenced by 12-month rainfall at a time lag of 12 months (Fig. 4a,b). Capture rates of both species were markedly higher when rainfall values approached 1000 mm. The two dasyurids, *N. yvonneae* and *S. murina*, showed no clear response to rainfall (Fig. 4c,d). Although the model for *S. murina* was statistically significant ( $P = 0.044$ ), graphical exploration of the data showed the effect size and explanatory power of the model was small.

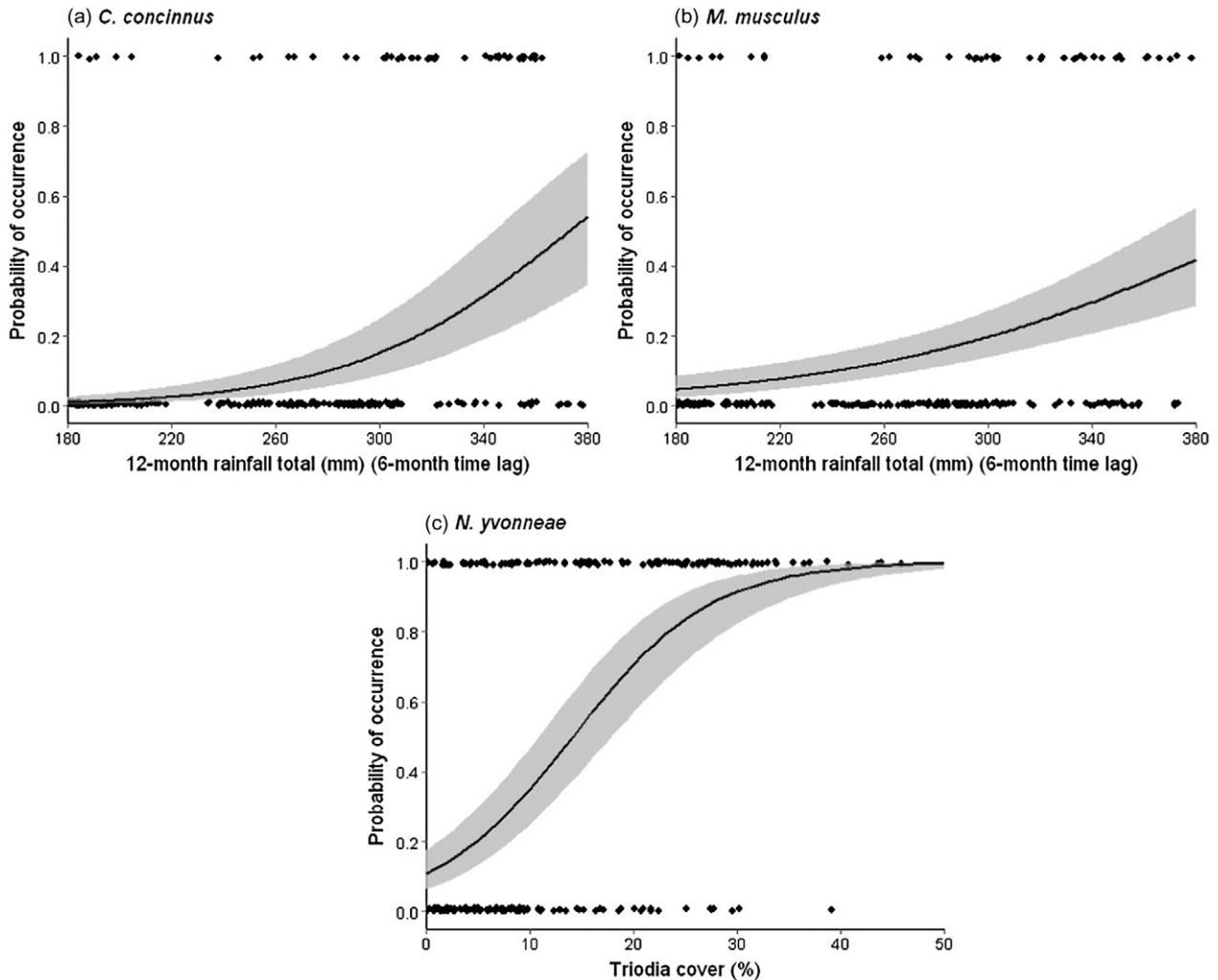
In 2012, *P. desertor* was recorded at Tarawi NR for the first time. Following a period of record high rainfall, the two captures of this species were the first in the Murray Mallee region since the 1850s.

## DISCUSSION

We investigated the drivers of small mammal distributions in semi-arid mallee ecosystems of southern Australia, using complementary broad-scale and long-term data. These results demonstrated that vegetation structure and rainfall are important drivers of small mammal distributions in mallee ecosystems. A key finding, however, was that the relative influence of these drivers was species-specific and could be related to life-history attributes of the small mammal species (see below).

### Drivers of small mammal distributions

At broad-scale survey sites, *C. concinnus* was more likely to occur following a year of above-average rainfall, with a time lag of 6 months. Vegetation structure also was influential: the occurrence of *C. concinnus* was positively associated with canopy height of eucalypts and the cover of hummock grass. It was largely absent

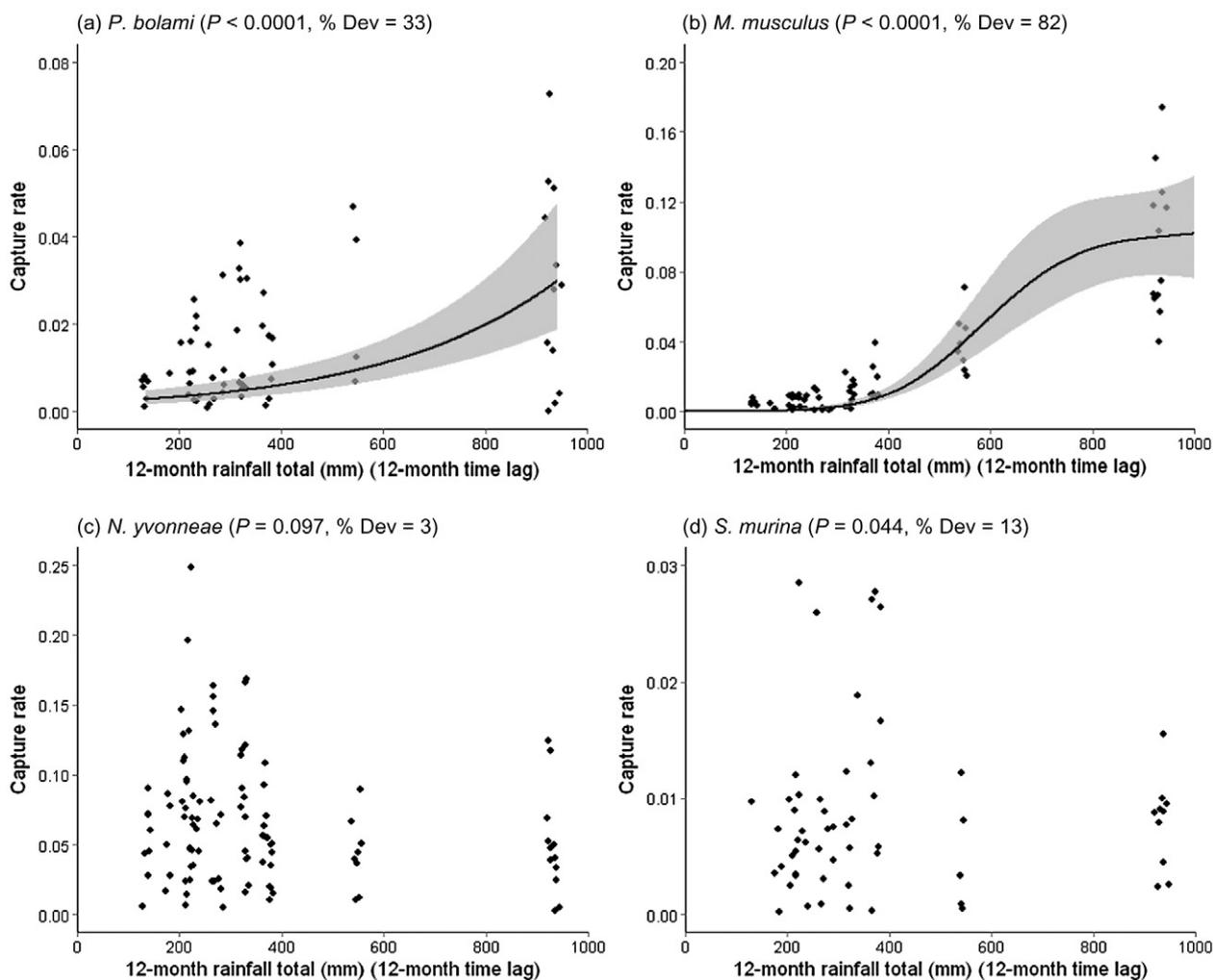


**Fig. 3.** Selected results from generalized additive mixed models of small mammal responses to broad-scale predictor variables. Solid lines represent model predictions, diamonds are observed data, shaded areas represent 95% confidence intervals.

from Tarawi NR (captured only twice in 15 years), and we could not model its response to rainfall at this location. In mallee ecosystems, high rainfall leads to an increase in primary productivity such as herb, grass and eucalypt growth (Noble & Vines 1993), which in turn can lead to an increase in invertebrate abundance and eucalypt flowering (Birtchnell & Gibson 2008). It is likely, therefore, that the association of *C. concinnus* with rainfall is driven by changes in food resources. We propose that higher capture rates of *C. concinnus* following high rainfall represented an increase in the abundance of regional populations, as well as a potential increase in the ‘trappability’ of individuals. *Cercartetus concinnus* can produce multiple litters throughout the year (Carthew *et al.* 2008), which would enable populations to increase rapidly when high-quality resources become more abundant. In addition, individuals can enter torpor for short periods

during times of stress (e.g. extreme weather) (Geiser 1987), and thus are more likely to be captured during favourable conditions.

Vegetation structure was clearly the strongest influence on the distribution of *N. yvonneae* at broad-scale sites. *Ningau yvonneae* was positively related to the cover of hummock grass; at sites containing no hummock grass, it was largely absent. Hummock grass offers a range of resources, including food, shelter and a suitable microclimate (Bos *et al.* 2002; Bos & Carthew 2003). These results were consistent with the responses of *N. yvonneae* to fire in mallee ecosystems, where it is typically absent from recently burnt vegetation with reduced ground cover (Kelly *et al.* 2010, 2011). Topography, floristic diversity and rainfall had little influence on the broad-scale occurrence of *N. yvonneae*, after considering vegetation structure. Further, analyses of long-term data provided little



**Fig. 4.** Small mammal responses to rainfall at Tarawi Nature Reserve (1997–2012). Capture rate = probability of success (capture of animal) for a single trap at a given site in a given survey period. % Dev = percentage deviance explained. Diamonds indicate observed data. The solid line represents regression model predictions, shaded areas represent 95% confidence intervals.

evidence of a relationship between *N. yvonneae* and rainfall. Capture rates of *N. yvonneae* also remained relatively high during periods of below-average rainfall, which occurred throughout much of the 15 years of data collection at Tarawi NR.

*Sminthopsis murina* was widespread and occurred at locations exhibiting a range of structural attributes; from dunes dominated by hummock grass to swales characterized by open vegetation. While rainfall had the strongest relative influence on its distribution at broad-scale survey sites, model fit was poor and offered little evidence that the variables measured were strong influences on its distribution at this scale. *Sminthopsis murina* showed no clear response to rainfall at Tarawi NR, following exceptionally high rainfall in 2011. Although *S. murina* appears to be a habitat generalist in mallee ecosystems, it is possible that

above-average rainfall at the right time (e.g. prior to the spring/summer breeding period) could positively influence populations.

Rainfall at a 6-month time lag was the strongest determinant of the presence of *M. musculus* at broad scales. Vegetation structure (a low canopy height) and floristic diversity (the presence of grasses and herbs) also were strong influences. Long-term data at Tarawi NR were consistent with the positive relationship with rainfall at broad scales. The positive relationship between *M. musculus* and rainfall is well documented in grain-growing areas of the Murray Mallee region (Singleton *et al.* 2005). In cropland, *M. musculus* increases episodically to plague proportions following high rainfall. Such outbreaks have been attributed to an increase in food supply leading to population increases (Singleton *et al.* 2001). In extensive mallee

vegetation, increases in *M. musculus* can also be attributed to a greater food supply of grasses, herbs, seeds and invertebrates.

At broad-scale survey sites, the native rodent *P. bolami* was rarely encountered, occurring at 18 of 280 sites. It was most common at Tarawi NR following a large rainfall event in 2000, and again in 2011/2012, with captures peaking 12 months after above-average rainfall. We interpreted this marked response to be a consequence of these long-term data spanning a greater range of rainfall conditions. In arid Australia, Moseby and Read (1999) similarly found that *P. bolami* numbers increased following rainfall.

### Comparisons with temperate and central arid regions

In temperate Australia, Fox (1982) developed a habitat accommodation model to explain a mammalian succession that develops in response to changes in vegetation structure, particularly following fire. Based on this model, we expected that vegetation structure would be a key determinant of small mammal distributions. Three of four species showed clear responses to vegetation structure, suggesting that it also plays an important role in shaping small mammal distribution in mallee ecosystems. However, for two of these species vegetation structure was a secondary influence, suggesting that the assemblage is not as strongly shaped by vegetation structure as in temperate environments.

There was little evidence for a predictable mammalian succession for this assemblage as a whole. Rather, several species showed marked variation in occurrence in response to temporal variation in rainfall (*C. concinnus*, *M. musculus*, *P. bolami*). Annual rainfall is much lower in mallee ecosystems than in temperate environments in Australia, and consequently small mammals occur at much lower densities (Bennett *et al.* 1989), they show more marked variation in capture rates depending on environmental conditions, and they appear to be more limited by rainfall-driven resources. While we did not specifically examine competition in this study – a key driver in temperate Australia – we expected competitive exclusion (if present) to be represented by clear differences in the habitat associations of each species. Such a pattern was not evident.

In arid Australia, Letnic *et al.* (2004) developed a state-and-transition model that highlights multiple states in the composition of assemblages of small mammals inhabiting hummock grassland. These states develop in response to rainfall-driven changes in food resources. Based on this model, we expected that rainfall would be a key determinant of small mammal

distributions in semi-arid mallee vegetation. Three of the five species modelled in this study showed a positive relationship with rainfall in at least one data set. Notably, the influence of rainfall differed between species and locations.

The strong influence of rainfall in both semi-arid and arid environments suggests similarities between the drivers of small mammal distributions in these two systems. Nevertheless, important differences remain. First, the rainfall regimes differ: although mean annual rainfall is typically higher in mallee vegetation, individual rainfall events and rainfall variability in central arid systems are larger. Letnic and Dickman (2010) indicated that large increases in small mammal populations in the arid zone occur following summer rains of at least 300 mm. In mallee ecosystems, such large rainfall events (and associated flooding) are rare and occurred only during the period of long-term data collection in 2010/2011. As a consequence, capture rates of small mammals in mallee ecosystems, following high rainfall, appear to be much lower than in arid environments where populations fluctuate to a greater degree. For example, in this study captures of *P. bolami* peaked at only seven captures per 100 trap nights. In arid Australia, the closely related sandy inland mouse *Pseudomys hermannsburgensis* was recorded at 20 captures per 100 trap nights following high rainfall (Dickman *et al.* 1999). In summary, the size of the ‘pulse’ in each system differs – due to differences in the size of rainfall events – which, in turn, leads to differences in the abundance of small mammals.

Second, the influence of vegetation structure appears to be stronger in mallee ecosystems than in arid hummock grassland. In semi-arid mallee, *N. yvonmeae* responded predictably to vegetation structure, and the distributions of *C. concinnus* and *M. musculus* were related, in part, to structural attributes. In arid systems also, members of the genus *Ningauia* are associated with high cover of *Triodia* hummocks (Haythornthwaite & Dickman 2006). Overall, however, the distribution of small mammals in arid Australia typically correlates poorly with vegetation structure (Letnic & Dickman 2010). Further, in mallee ecosystems, habitat attributes such as *Triodia* cover, litter depth and canopy height show evidence of directional change following fire over a timescale of decades (Haslem *et al.* 2011); whereas key structural attributes in arid hummock grassland undergo more frequent changes over shorter time periods (Letnic & Dickman 2010).

### Influence of life-history traits

Conceptual models developed to describe small mammal communities in either temperate Australia or arid Australia are not adequate, on their own, for small

mammal communities in mallee ecosystems. Having identified the relative influence of vegetation structure, floristic diversity, topography and rainfall – and found that the relative influence was species-specific – consideration of the known life-history attributes of each species provides useful insights into the observed responses.

Four species of rodents were captured in mallee vegetation: *M. musculus*, *N. mitchelli*, *P. bolami* and *P. desertor*. Each of these has relatively flexible life-history traits: an opportunistic breeding strategy, high reproductive potential, a generalist diet and the ability to burrow in sandy soils. Two of these species responded strongly to rainfall, and it is likely that *N. mitchelli* also responds to rainfall driven-food pulses (Breed *et al.* 2008). The flexibility in rodent life histories means that they can respond rapidly to rainfall-driven changes in food (e.g. seeds and herbage) (see also Dickman *et al.* 1999).

Two species of burramyids occur in mallee ecosystems: *C. concinnus* and *C. lepidus*. Pygmy possums are opportunistic breeders (Ward 1990); for example, *C. concinnus* can produce three litters of six young per year (Menkhorst & Knight 2004). Their diet is broad, but consists substantially of a resource that pulses: *Eucalyptus* pollen and nectar (Pestell & Petit 2007). Their life-history appears geared for responding to pulsed resources, and consequently it is not surprising that there was a clear relationship between rainfall and *C. concinnus* in this study. Population dynamics of other marsupial nectarivores have also been linked with rainfall patterns (Wooller *et al.* 1998).

The two dasyurids commonly encountered in mallee vegetation, *N. yvonneae* and *S. murina*, employ different life-history strategies. *Ningau* *yvonneae* has a relatively restricted life-history: it is typically monoestrous (breeding annually in spring) and feeds largely on invertebrates (Bos & Carthew 2001). It showed either no response or limited response to rainfall. Restricted seasonal breeding is likely to inhibit a dramatic response to rainfall, as has been shown for insectivorous dasyurids in the arid zone (Dickman *et al.* 2001). In contrast, *S. murina* has a more flexible life-history: it is polyoestrous and can breed in spring and summer. Although some studies in temperate Australia link *S. murina* with vegetation characteristics at local scales (Monamy & Fox 2005), regional populations are often patchily distributed and temporally dynamic (Fox 1996). It feeds on invertebrates and so is unlikely to respond to rainfall as markedly as rodents, which feed directly on vegetative products of a rainfall-driven increase in primary productivity. Further work is required to establish whether, for dasyurids, rainfall-driven pulses at the right time of year are required to stimulate a response.

In summary, species responses are consistent with their known life-history characteristics, which provide

a useful way to synthesize observed responses (Friend 1993). Opportunistic breeders show a more marked response to rainfall-driven changes in food resources, whereas seasonal breeders show a less consistent response. The species with the least flexible life-history – *N. yvonneae* – is most closely associated with vegetation structure.

## CONCLUSIONS

An important feature of this study was the complementary use of broad-scale and long-term data sets. Using broad scale survey data enabled a test of the consistency and robustness of relationships at large spatial scales. Using long-term data enabled examination of the effects of temporal variation in rainfall, which spanned a greater range of climatic variability than occurred during the broad-scale survey. Consistent findings between data sets adds strength to observed relationships, such as that between the distribution of *M. musculus* and rainfall. In other cases, these complementary data sets provided unique insights into the distribution of species, such as for *P. bolami*, which was uncommon during the broad-scale survey. The large-scale spatial and temporal variability of small mammal populations in semi-arid mallee ecosystems means that the extensive remaining blocks of vegetation are particularly important for the long-term conservation of the region's small mammal assemblage.

## ACKNOWLEDGEMENTS

Thanks to John Warren (New South Wales National Parks and Wildlife Service (NPWS)) who provided invaluable assistance to RD over many years of surveys, and to Andrew Willson (NPWS) who contributed to the establishment of the Tarawi NR pitfall sites. Funding for the Mallee Fire and Biodiversity Project (MFBP) was provided by Land and Water Australia, Department for Environment and Heritage (South Australia), Parks Victoria, Department of Sustainability and Environment (Victoria), Mallee Catchment Management Authority, NPWS, Department of Environment and Climate Change (New South Wales), Lower Murray–Darling Catchment Management Authority, Natural Heritage Trust, Birds Australia, Australian Wildlife Conservancy and the Murray Mallee Partnership. We are grateful to the Doyle and Barnes families for access to Petro and Lethero Stations, respectively. Thanks to Lauren Brown, Kate Callister, Lisa Spence-Bailey and all members of the MFBP; the volunteers who assisted with fieldwork; and the organizers of the symposium 'The Greening of Arid Australia'.

## REFERENCES

- Australian Bureau of Meteorology (2012) [Cited August 2012.] Available from URL: <http://www.bom.gov.au/>
- Bennett A. F., Lumsden L. F. & Menkhorst P. W. (1989) Mammals of the mallee region of south-eastern Australia. In: *Mediterranean Landscapes in Australia: Mallee Ecosystems and Their Management* (eds J. C. Noble & R. A. Bradstock) pp. 191–220. CSIRO, Melbourne.
- Bennett A. F., Lumsden L. F. & Menkhorst P. W. (2006) Mammals of the Mallee Region, Victoria: past, present and future. *Proc. R. Soc. Vic.* **118**, 259–80.
- Birtchnell M. J. & Gibson M. (2008) *Flowering Ecology of Honey-Producing Flora in South-East Australia*. Australian Government. Rural Industries Research and Development Corporation, Canberra.
- Bos D. G. & Carthew S. M. (2001) Population ecology of Ningau yvonneae (Dasyuridae : Marsupialia) in the Middleback Ranges, Eyre Peninsula, South Australia. *Wildl. Res.* **28**, 507–15.
- Bos D. G. & Carthew S. M. (2003) The influence of behaviour and season on habitat selection by a small mammal. *Ecography* **26**, 810–20.
- Bos D. G., Carthew S. M. & Lorimer M. F. (2002) Habitat selection by the small dasyurid *Ningau yvonneae* (Marsupialia : Dasyuridae) in South Australia. *Austral Ecol.* **27**, 103–9.
- Breed W. G., Carthew S. M. & Bradley C. (2008) Mitchell's Hopping Mouse *Notomys mitchelli* (Ogilby, 1838). In: *The Mammals of Australia*, 3rd edn (eds S. Van Dyck & R. Strahan) pp. 607–8. Reed New Holland, Chatswood.
- Brown J. H. (1995) *Macroecology*. The University of Chicago Press, Chicago, IL.
- Brown J. H. & Ernest S. K. M. (2002) Rain and rodents: complex dynamics of desert consumers. *Bioscience* **52**, 979–87.
- Burnham K. P. & Anderson D. R. (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.
- Carthew S. M., Cadzow B. R. & Foulkes J. N. (2008) Western pygmy-possum *Cercartetus concinnus* (Gould, 1845). In: *The Mammals of Australia*, 3rd edn. (eds S. V. Dyck & R. Strahan) pp. 215–7. Reed New Holland, Chatswood.
- Dickman C. R., Greenville A. C., Tamayo B. & Wardle G. M. (2011) Spatial dynamics of small mammals in central Australian desert habitats: the role of drought refugia. *J. Mammal.* **92**, 1193–209.
- Dickman C. R., Haythornthwaite A. S., McNaught G. H., Mahon P. S., Tamayo B. & Letnic M. (2001) Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildl. Res.* **28**, 493–506.
- Dickman C. R., Mahon P. S., Masters P. & Gibson D. F. (1999) Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildl. Res.* **26**, 389–403.
- Elith J., Leathwick J. R. & Hastie T. (2008) A working guide to boosted regression trees. *J. Anim. Ecol.* **77**, 802–13.
- Fox B. J. (1982) Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* **63**, 1332–41.
- Fox B. J. (1996) Long-term studies of small-mammal communities from disturbed habitats in eastern Australia. In: *Long-Term Studies of Vertebrate Communities* (eds M. L. Cody & J. A. Smallwood) pp. 467–501. Academic Press, San Diego, CA.
- Fox B. J., Taylor J. E. & Thompson P. T. (2003) Experimental manipulation of habitat structure: a retrogression of the small mammal succession. *J. Anim. Ecol.* **72**, 927–40.
- Friend G. R. (1993) Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biol. Conserv.* **65**, 99–114.
- Geiser F. (1987) Hibernation and daily torpor in 2 pygmy possums (*Cercartetus* spp, Marsupialia). *Physiol. Zool.* **60**, 93–102.
- Haslem A., Kelly L. T., Nimmo D. G. *et al.* (2011) Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *J. Appl. Ecol.* **48**, 247–56.
- Haythornthwaite A. S. & Dickman C. R. (2006) Distribution, abundance, and individual strategies: a multi-scale analysis of dasyurid marsupials in arid central Australia. *Ecography* **29**, 285–300.
- Holland G. J. & Bennett A. F. (2007) Occurrence of small mammals in a fragmented landscape: the role of vegetation heterogeneity. *Wildl. Res.* **34**, 387–97.
- Holmgren M., Stapp P., Dickman C. R. *et al.* (2006) Extreme climatic events shape arid and semiarid ecosystems. *Front. Ecol. Environ.* **4**, 87–95.
- Kelly L. T., Nimmo D. G., Spence-Bailey L. M., Clarke M. F. & Bennett A. F. (2010) The short-term responses of small mammals to wildfire in semiarid mallee shrubland, Australia. *Wildl. Res.* **37**, 293–300.
- Kelly L. T., Nimmo D. G., Spence-Bailey L. M. *et al.* (2011) The influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Divers. Distrib.* **17**, 462–73.
- Kelly L. T., Nimmo D. G., Spence-Bailey L. M. *et al.* (2012) Managing fire mosaics for small mammal conservation: a landscape perspective. *J. Appl. Ecol.* **49**, 412–21.
- Kelt D. A. (2011) Comparative ecology of desert small mammals: a selective review of the past 30 years. *J. Mammal.* **92**, 1158–78.
- Letnic M. & Dickman C. R. (2010) Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biol. Rev.* **85**, 501–21.
- Letnic M., Dickman C. R., Tischler M. K., Tamayo B. & Beh C. L. (2004) The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *J. Arid Environ.* **59**, 85–114.
- Menkhorst P. & Knight F. (2004) *A Field Guide to the Mammals of Australia*, 2nd edn. Oxford University Press, Melbourne.
- Menkhorst P. W. & Bennett A. F. (1990) Vertebrate fauna of mallee vegetation in southern Australia. In: *The Mallee Lands: A Conservation Perspective* (eds J. C. Noble, P. J. Joss & G. K. Jones) pp. 39–53. CSIRO, Melbourne.
- Meserve P. L., Kelt D. A., Milstead W. B. & Gutierrez J. R. (2003) Thirteen years of shifting top-down and bottom-up control. *Bioscience* **53**, 633–46.
- Monamy V. & Fox B. J. (2005) Differential habitat use by a local population of subadult common dunnarts, *Sminthopsis murina*, following wildfire in coastal wet heath, New South Wales, Australia. *Wildl. Res.* **32**, 617–24.
- Monamy V. & Fox B. J. (2010) Responses of two species of heathland rodents to habitat manipulation: vegetation density thresholds and the habitat accommodation model. *Austral Ecol.* **35**, 334–47.

- Morton S. R., Stafford Smith D. M., Dickman C. R. *et al.* (2011) A fresh framework for the ecology of arid Australia. *J. Arid Environ.* **75**, 313–29.
- Moseby K. E. & Read J. L. (1999) Population dynamics and movement patterns of Bolam's Mouse, *Pseudomys bolami*, at Roxby Downs, South Australia. *Austral. Mammal.* **20**, 353–68.
- Noble J. C. (1984) Mallee. In: *Management of Australia's Rangelands* (eds G. N. Harrington, A. D. Wilson & M. D. Young) pp. 223–40. CSIRO, Melbourne.
- Noble J. C. & Vines R. G. (1993) Fire studies in mallee (*Eucalyptus* spp.) communities of western New South Wales: grass fuel dynamics and associated weather patterns. *Rangeland J.* **15**, 270–97.
- Ojeda R. A., Tabeni S. & Corbalán V. (2011) Mammals of the Monte Desert: from regional to local assemblages. *J. Mammal.* **92**, 1236–44.
- Pearce J. & Ferrier S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* **133**, 225–45.
- Pestell A. J. L. & Petit S. (2007) Diet of the western pygmy possum, *Cercartetus concinnus* Gould (Marsupialia: Burramyidae), at Innes National Park, South Australia, and evaluation of diet sampling methods. *Austral. J. Zool.* **55**, 275–84.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Singleton G., Krebs C. J., Davis S., Chambers L. & Brown P. (2001) Reproductive changes in fluctuating house mouse populations in southeastern Australia. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 1741–8.
- 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. *Biol. J. Linn. Soc.* **84**, 617–27.
- Southgate R. & Masters P. (1996) Fluctuations of rodent populations in response to rainfall and fire in a central Australian hummock grassland dominated by *Plectrachne schinzii*. *Wildlife Research* **23**, 289–303.
- Ward S. J. (1990) Reproduction in the western pygmy-possum, *Cercartetus concinnus* (Marsupialia: Burramyidae), with notes on reproduction of some other small possum species. *Wildl. Res.* **38**, 423–38.
- Wood S. N. (2006) *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC Press, Boca Raton, FL.
- Wooler R. D., Richardson K. C., Garavanta C. A. M., Saffer V. M., Anthony C. & Wooler S. J. (1998) The influence of annual rainfall upon capture rates of a nectar-dependent marsupial. *Wildl. Res.* **25**, 165–9.
- Zuur A. F., Ieno E. N., Walker N. J., Saveliev A. A. & Smith G. M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Candidate predictor variables for modelling small mammal distributions.