

Making the most of incomplete long-term datasets: the MARSS solution

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ABSTRACT

Long-term field-based monitoring is essential to develop a deep understanding of how ecosystems function and to identify species at risk of decline. However, conducting long-term field-based research poses some unique challenges due to the harsh environmental conditions or extreme weather events that may be encountered. Such conditions are especially likely to occur in arid environments. Fieldwork issues can arise from vehicle breakdowns, wildfires and heavy rainfall events, all of which can delay or even cancel data collection. In addition, long-term monitoring typically requires multiple observers, which may add observation bias to estimates of measured parameters. Thus there is an increasing need to develop new statistical techniques that take advantage of the power of long time-series datasets that also are incomplete. Here we discuss multivariate autoregressive state-space (MARSS) modelling; a relatively new statistical technique for modelling long-term time-series data. MARSS models allow users to investigate incomplete datasets caused by missing values. In contrast to traditional modelling techniques, such as generalised linear models that only estimate error from environmental stochasticity (process error), MARSS models estimate both process and observation errors. By estimating observation errors, researchers can incorporate bias from different observers and methods into population or other parameter estimates. To illustrate the MARSS technique we interrogate long-term animal and plant datasets from arid central Australia that contain missing values and were collected by multiple observers. We then discuss the findings from the MARSS models and their implications for management. Lastly, we suggest future applications that this technique could be used for, such as studies of animal movements and food webs.

Key words: MARSS, long-term monitoring, Simpson Desert, observation error, process error, spatial dynamics, populations

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Introduction

Long-term field-based monitoring is essential to accurately describe population fluctuations and cycles (Wardle *et al.* 2013) as well as environmental changes (Lindenmayer *et al.* 2012 and articles in this issue). As we enter the Anthropocene, long-term monitoring of species' populations and ecological processes provides valuable insights for managing species in decline by acting both as an early warning system and identifying threats that can be managed. However, field-based monitoring can be costly and also prone to delays and incomplete sampling due to variable and often inclement environmental conditions and insufficient funding. Nonetheless, the temporal depth of long-term field data is its strength, and new statistical tools are now available to provide better population and other parameter estimates, even with incomplete datasets.

Field-based researchers regularly undertake research trips to remote locations and have to endure difficult

environmental conditions. For example, rainfall, heat, wildfires, equipment failure and vehicle mishaps are a few among many problems that can delay or even cancel data collection. Field work issues are so common that ecologists and biologists took to Twitter in 2015–2017 and shared their entertaining 'fieldwork fail' moments (Figure 1). The thousands of stories generated great media interest (Shaw 2015), new websites (www.fieldworkfail.com) and a book successfully funded on Kickstarter (www.kickstarter.com). The likelihood of experiencing fieldwork problems increases over time when undertaking regular and repeated field-based research, and thus long-term datasets will often have missing values. Traditional solutions for handling missing data centre around pair-wise deletion to ensure balanced sample sizes and simplify subsequent analyses (Boehmke 2016; Nakagawa and Freckleton 2008). Given that field data are hard-won and expensive to collect, this is

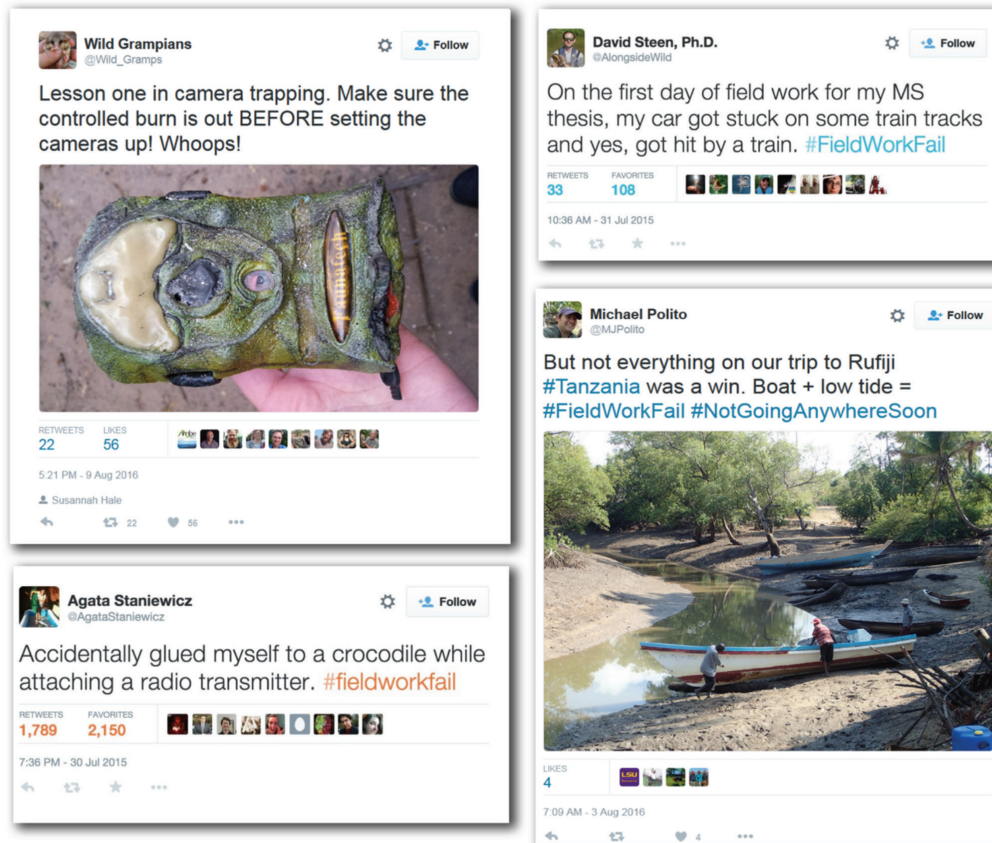


Figure 1: Four example tweets from #FieldWorkFail illustrating the many stories and fieldwork issues that biologists and ecologists encounter during their monitoring programs.

inefficient and reduces statistical power (Nakagawa and Freckleton 2008). If missing values occur in a non-random pattern, such as during extreme weather events, then potential bias can be introduced (Nakagawa and Freckleton 2008). Alternative techniques replace missing values with 'best guesses', such as using the mean or median of the surrounding values, but may fail to capture the true population or parameter variability.

Successful long-term research programs train many students and volunteers. For example, the Desert Ecology Research Group (DERG) at the University of Sydney has trained more than 40 Honours and higher research degree students and >900 volunteers over 29 years (Dickman *et al.* 2014). Many of these people have gone onto employment armed with field-based research skills. The DERG research program trains a core team in key data observations and frequently calibrates the observations across the staff. However, like many other long-term programs, the program now has potentially heterogeneous data owing to these different observers who participated in data-collection. Multiple observers increase the chance of observer error and can introduce significant bias. For example, Blackwell *et al.* (2006) estimated that observer error from taking standard morphological measurements on mammals was up to 40%, even on dead specimens. Blackwell *et al.* (2006) concluded that repeated

measurements should be taken on individual animals, significantly reducing observer error. Rigorous training in data collection and entry can also minimise observer error (Hannaford *et al.* 1997; Thompson and Mapstone 1997) and is strongly recommended. However, the decline in research funding globally (Van Noorden and Brumfiel 2010) is putting severe pressure on research projects, and particularly so for long-term research (Lindenmayer *in press*; Lindenmayer *et al.* 2017). Taking repeated measurements is time-consuming and costly, and usually abandoned in favour of greater replication. In addition, insufficient funding can increase observation error, for example, by reducing survey effort and thus accuracy and precision in censusing populations (Ahrestani *et al.* 2013; Morellet *et al.* 2007). Hence, it is now becoming increasingly necessary to account for observation error in statistical models to gain accurate estimates (Box 1).

Here, we discuss a new and exciting statistical technique: multivariate autoregressive state-space (MARSS) modelling. MARSS models can be used to provide accurate population or parameter estimates using temporal datasets that are incomplete and that have engaged multiple observers. Below, we briefly describe the technique and then illustrate it with case studies from long-term monitoring (up to 22 years) of desert animals and plants in central Australia. We uncover the spatial dynamics of sub-populations of six species of animals and

Box 1: Process and observation error

Ecologists and population biologists aim to get accurate estimates of a species' true population size. However, the data they collect on species commonly contain two forms of error. Process error represents temporal variability in population size due to environmental and demographic stochasticity (Figure 1). Observation error represents sampling error, such as temporal changes in detectability, error resulting in only a sub-sample of the population being counted, error introduced from multiple observers, or a combination of all three (Figure 1). These two forms of error mask the actual population numbers, but are contained in all datasets. This problem was first recognised in the aerospace industry and researchers of systems theory, where the state-space models were the basis of guidance control and radar systems (Hutchinson 1984). Famous examples of the use of state-space models, include the Apollo and Polaris programs (see Hutchinson 1984). They are used throughout ecology to analyse movement data (e.g. Patterson *et al.* 2008), population size (Royle and Dorazio 2008), species interactions and ecological processes (e.g. Lindegren *et al.* 2009).

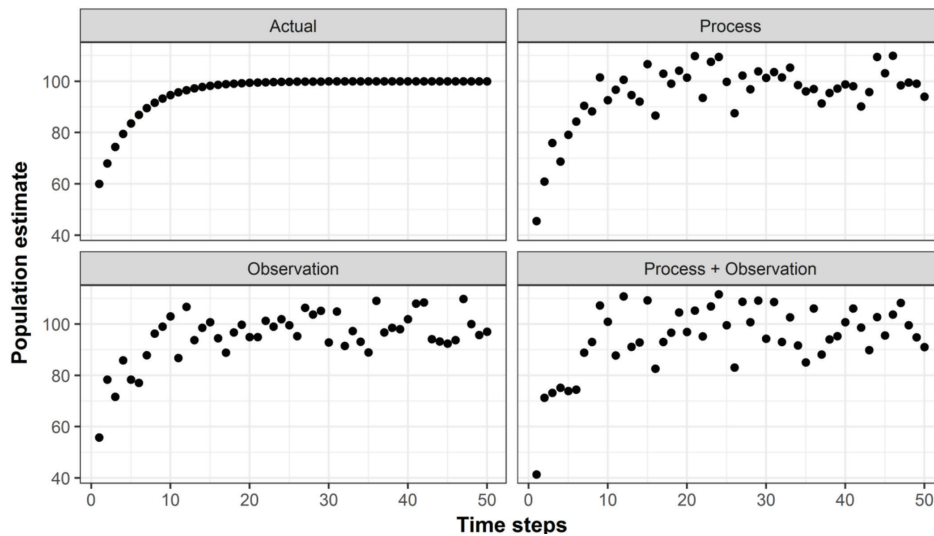


Figure 1: Ecologists want to know the actual or underlying population process, or processes, but data collected from the field will have both process and observation errors.

one species of plant in nine widely separated sites across the 8000 km² study region. In addition, we use MARSS models to discover the influence of drivers, such as rainfall and wildfire, on these populations. Lastly, we discuss the implications of the findings from MARSS models for management and provide examples for future directions.

The MARSS solution

Traditionally, investigations of the spatial structure of species' populations have been approached in two broad ways. Firstly, different populations were defined by grouping survey sites together and testing for any difference between the group's means (e.g. Haythornthwaite and Dickman 2006). However, often analyses were snap-shot events and each time interval would be analysed separately. A repeated measures design can be used, but both the snap-shot approach and repeated measures approach do not take full advantage of all the information captured in time-series datasets, such as the temporal autocorrelation, which can provide valuable information about a population's density dependence (Berryman and Turchin 2001). Auto-regressive linear models were then developed, but they did not extend beyond a single population (Berryman

1999). Lastly, questions on population synchrony were tested by computing Pearson cross-correlations between two or more populations (Bjørnstad *et al.* 1999). Pearson product-moment correlations are performed using the first-difference time series of log-abundance, which reflects the synchrony of the population growth rates (Bjørnstad *et al.* 1999). This method is simple to compute, and interpretation is based on the sign and magnitude of the correlation coefficient; however, the researcher must define the boundaries of the correlation coefficient that correspond to spatial synchrony. It also does not allow for other population structures or their covariates to be tested. Both of the above techniques assume that only process (environmental) errors are important, and both can be sensitive to missing values.

MARSS models allow the hierarchical modelling of multiple populations or methods and their parameters, such as density-dependence, while including both process (state) and observation variability (Ward *et al.* 2010). Process variability represents temporal variability in population size due to environmental and demographic stochasticity (Ward *et al.* 2010). Observation variability includes sampling error (e.g., temporal changes in

detectability or error resulting in only a sub-sample of the population being counted) (Hinrichsen and Holmes 2009; Ward *et al.* 2010). Both forms of error occur in field data collected by ecologists, and we must partition and account for these errors to obtain accurate estimates of actual population size (Box 1). There are two models—the process and observational model—that together make up the MARSS model. Observations or survey data are entered into the observation model where the ‘true’ population size and observation error are estimated. Then the ‘true’ population estimate is entered into the process model, along with any covariates, and the population parameters (growth rates and density dependence) and process errors are estimated (Box 2).

We based the MARSS models for our study species on the Gompertz population growth model (Box 2) and assumed that sub-population growth rate varied exponentially with sub-population size, and that the sub-populations are closed to immigration and emigration (Hinrichsen and Holmes 2009). We use the term ‘sub-population’ here to connote groups of individuals of each of the study species in the nine survey sites. Although the Gompertz model fitted our data well, other population growth models can be used. The models are autoregressive and thus incorporate the previous population estimate into the current time period and allow population growth rates to be calculated. In the examples below we use both frequentist (case study 1)

and Bayesian techniques (case study 2) to illustrate the versatility of MARSS models. The first case study using frequentist approaches was conducted in R 3.03 (R Core Team 2017) using the package MARSS v 3.4 (Holmes *et al.* 2013; Holmes *et al.* 2014; Holmes *et al.* 2012). The second case study used Bayesian methods and was analysed using R 3.03 and JAGS 3.4.0 (Plummer 2013), using the R2jags 0.04-03 (Su and Yajima 2014) and rjags 3-13 (Plummer 2014) packages. MARSS models are best used with long-term time-series data (> 10 time-steps); further information on these models can be found in Newman *et al.* (2014), Holmes *et al.* (2012) and Hinrichsen and Holmes (2009).

MARSS models can incorporate datasets with missing values and can model likely values. They have been used successfully to investigate different spatial population dynamics (Greenville *et al.* 2016a; Greenville *et al.* 2016b; Nguyen *et al.* 2015; Ward *et al.* 2010), model species and ecological interactions (Walsh *et al.* 2016), and incorporate different life-history traits and observation errors from different methods (Nguyen *et al.* 2015). The two case studies below have datasets, including covariates, that contain missing data (annual surveys not completed for individual sites ranged from 1–9 years) and multiple observers over the past 17–22 years. The MARSS equations and detailed descriptions of the modelling approach are provided in Greenville *et al.* (2016a, b) and Nguyen *et al.* (2015).

Box 2: Multivariate autoregressive state-space (MARSS) modelling

MARSS models are hierarchical state-space models that include both process (state) and observation variability (Ward *et al.* 2010). The process component is a multivariate first-order autoregressive process and is written in log-space (Holmes *et al.* 2014; 2012) as:

$$\mathbf{X}_t = \mathbf{B}\mathbf{X}_{t-1} + \mathbf{c}\mathbf{C}_t + \mathbf{u} + \mathbf{w}_t; \quad \mathbf{w}_t \sim \text{MVN}(\mathbf{0}, \mathbf{Q}) \quad (1)$$

where \mathbf{X}_t represents a vector of all m sub-populations (up to nine sub-populations for each species) at time t (year), and \mathbf{u} is a vector of length m . \mathbf{B} and \mathbf{Q} are matrices that denote process parameters. The \mathbf{B} diagonal elements (B_{ii}) represent the coefficients of autoregression in the populations through time and represent the strength of density dependence (diagonal element $B_{ii} = 1$ represents density independence, $B_{ii} < 1$ = density dependence). The off-diagonal elements in the \mathbf{B} matrix allow for interactions between processes, such as between species populations (Holmes *et al.* 2014). The parameter \mathbf{u} describes the trend of the sub-population. \mathbf{C}_t represents covariates through time t and \mathbf{c} are the coefficients of the covariates through time. \mathbf{w}_t denotes process errors, which we assumed to be independent and to follow a multivariate normal distribution with a mean of zero and variance-covariance matrix \mathbf{Q} (i.e., \mathbf{Q} diagonals represent process variance and off-diagonals represent how the sub-populations are correlated to one another).

The observation component, written in log-space (Holmes *et al.* 2014; 2012), is:

$$\mathbf{Y}_t = \mathbf{Z}\mathbf{X}_t + \mathbf{a} + \mathbf{v}_t; \quad \mathbf{v}_t \sim \text{MVN}(\mathbf{0}, \mathbf{R}) \quad (2)$$

where \mathbf{Y}_t represents a vector of all observations at n sites at time t , \mathbf{a} denotes the mean bias between sites, and \mathbf{Z} is an $n \times m$ matrix of 0s and 1s that assigns observations to a sub-population structure. The number of sites (n) may be different from the number of sub-populations (m) at time t (Ward *et al.* 2010). Observation errors, \mathbf{v}_t , are assumed to be uncorrelated and follow a multivariate normal distribution, with a mean of zero and a variance-covariance matrix \mathbf{R} . Equations (1) and (2) comprise the MARSS model.

Case studies

1. Spatial dynamics of spinifex grasslands

Vegetation cover has strong relationships with global environmental drivers such as atmospheric CO₂ (Braswell *et al.* 1997), water balance (Joffre and Rambal 1993), land management practices (Vicente-Serrano *et al.* 2004) and fire return intervals (Eckhardt *et al.* 2000). Monitoring of vegetation cover often relies on visual inspection of fixed plots to estimate cover (i.e., cover as a percentage of the total plot area), and is a quick method to use. However, visual methods are highly susceptible to observation error, raising concerns about the reliability and repeatability of visual estimates (Helm and Mead 2004).

Our field studies were carried out on Ethabuka Reserve (23° 46' S, 138° 28' E) and three neighbouring properties (Cravens Peak Reserve, Carlo and Tobermorey stations) in the north-eastern Simpson Desert, western Queensland. Linear red sand dunes are the major landform of the desert and are dominated by hard spinifex, *Triodia basedowii* (E.Pritz., Poaceae). We used a MARSS approach to describe the spatial structure of populations of this spinifex across the nine widely distributed sites, and to account for observation error arising from our visual estimation methods. Based on previous experience, we expected that spinifex cover would be affected by rainfall and wildfire, and that the structure of sub-populations might show several different dynamic patterns across the nine sites. Specifically, we used MARSS models to test the hypotheses that sub-populations of spinifex: (1) exhibit regional synchrony (i.e., cover varies over time in the same way across sites); (2) are asynchronous (cover varies over time in different ways across sites); (3) form two sub-populations at burnt versus unburnt sites (wildfire hypothesis); or (4) form three sub-populations that vary according to their location within shared rainfall gradients (productivity hypothesis). Tests of wildfire and population parameters were considered significant if the 95% confidence interval (CI) did not cross zero. Further details and explanations behind the generation of the above hypotheses can be found in Nguyen *et al.* (2015).

Study species

Spinifex (*Triodia* spp.) grasslands occupy nearly one third of the Australian continent (Wardle and Nano 2017), in areas receiving 125–500 mm of annual rainfall (Nano *et al.* 2012; Winkworth 1967). Spinifex is highly flammable (Allan and Southgate 2002) and readily burns in the study region after large and flooding rainfall events (Greenville *et al.* 2009). *Triodia basedowii* does not regenerate vegetatively after fire and primarily regenerates by seed germination (Westoby *et al.* 1988). Flowering and seeding respond predominately to spring and summer rains when mass mast seeding events can occur (Westoby *et al.* 1988; Wright *et al.* 2014).

Field methods

Spinifex cover was scored visually by multiple observers as the percentage cover within quadrats of 2.5 m radius. Data were then converted to m² to allow comparisons with other studies. Field sampling was carried out from 1990 to 2013 at one site and at eight other sites from 1995 to 2013. Each site contained 2–12 1-ha grids spaced 0.5–2 km apart in randomly chosen positions along access tracks; six spinifex sampling quadrats were established on each grid. Sampling was conducted at irregular intervals from 2 to 6 times a year and, when sites could not be surveyed, missing values were included in the time-series. As sampling did not begin at most sites (8 of 9) until 1995, we use data from 1995 onwards. Data were aggregated by year to account for the time needed for spinifex growth to respond to rainfall (Nguyen *et al.* 2015).

Fire treatment was allocated retrospectively, whereby a site was labelled as burnt if most sampling grids experienced a fire during the study period (six of nine sites). In such cases, grids that were unaffected by fire for that site were discarded for analyses. Likewise, for sites labelled as unburnt, grids that did experience a fire were discarded. A more detailed summary of methods and site assignment can be found in Nguyen *et al.* (2015) and Dickman *et al.* (2014).

Results

The best supported MARSS population model for spinifex was the wildfire model (Nguyen *et al.* 2015), suggesting that populations of this species are structured into two sub-populations across the study region depending on the recent history of wildfire (Figure 2). Wildfire had a significant effect on spinifex cover (-5.65, CI: -0.68 – -4.02). Cover estimates produced by the wildfire model indicate gradually increasing cover from 1995 onwards across all sites until wildfires in 2001–2002 when cover declined dramatically, creating a distinct division between the burnt and unburnt populations (Figure 2). Spinifex cover in unburnt sites followed similar trends from 1995 to 2002 and then decreased until 2008 due to drought (Nguyen *et al.* 2015).

Process error was lower for spinifex cover in burnt sites (0.119, CI: 0 – 0.60) than unburnt sites (0.91, CI: 0.001 – 2.06). Observation error was higher than both process errors (1.47, CI: 0.91 – 1.67). There was no difference between spinifex growth rates in burnt (0.18, CI: -0.07 – 0.41) and unburnt sites (0.06, CI: -0.49 – 0.46).

2. Spatial dynamics of desert mammals and reptiles

Understanding the temporal and spatial dynamics of species populations remains a key focus of population biology, providing vital insight into the drivers that

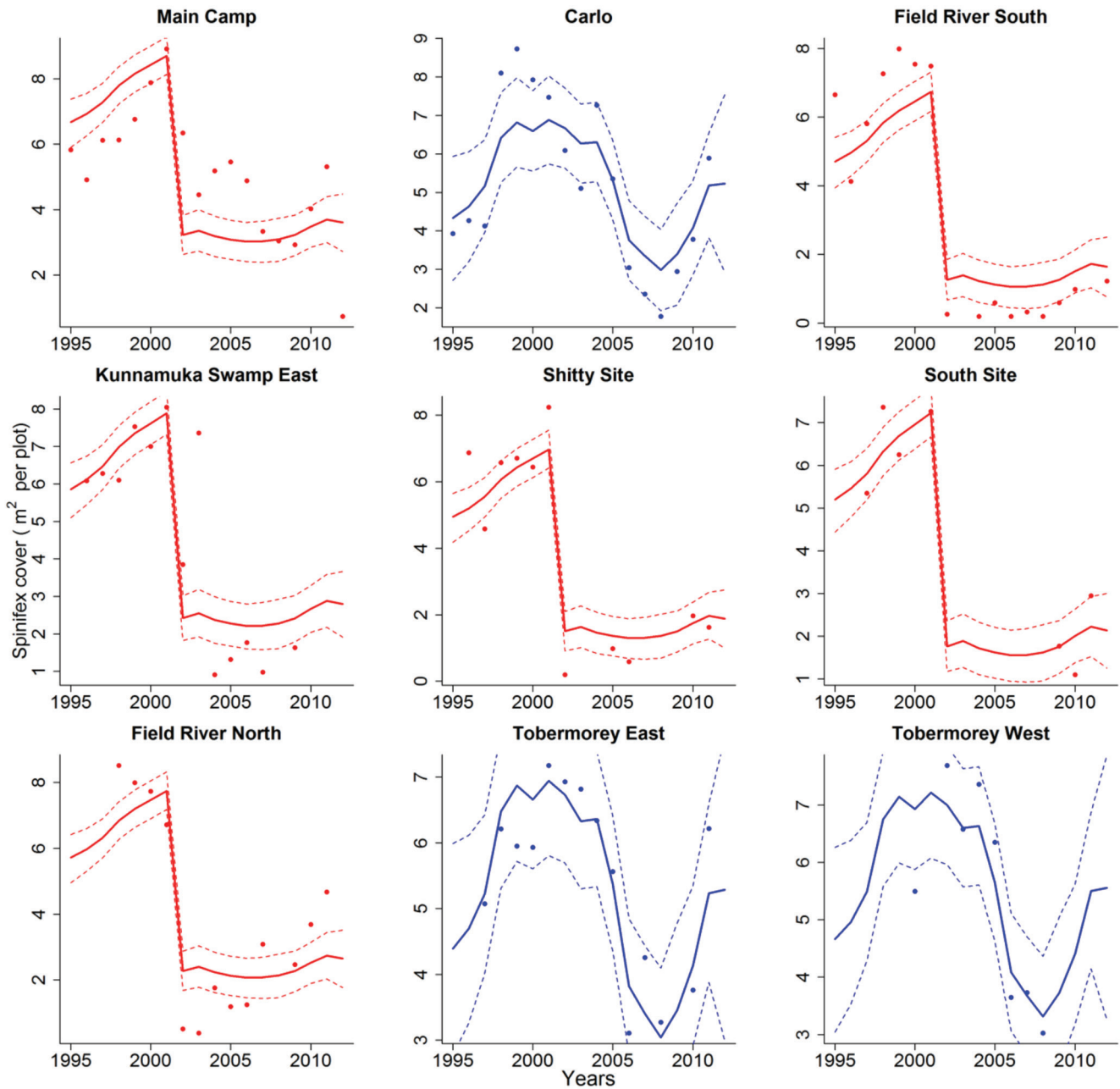


Figure 2: Predicted population sizes (lines) and visual cover observations (dots) and their 95 % confidence intervals (dashed lines) for cover of spinifex from wildfire model from nine sites in the Simpson Desert, central Australia. Red represents predictions and observations from burnt sites, while blue represents those from unburnt populations. Figure reproduced with kind permission from Nguyen *et al.* (2015). *Plant Ecol.* **216**: 975-88.

influence demography and into sub-populations that are vulnerable to extinction (Heino *et al.* 1997). Using long-term population data (17-22 years) on three species of small mammals and three species of reptiles at our nine widely separated sites in the Simpson Desert, we first tested the hypothesis that annual rainfall drives regional synchrony in the dynamics of the study species. For species that did not exhibit synchrony, we then explored how the dynamics of the sub-populations varied across the nine study sites. Based on previous experience, and similar to the example using spinifex, above, we considered four different dynamical patterns to be plausible. These were that sub-populations of our study species: 1) exhibit

asynchrony (i.e., all sub-populations fluctuate out of synchrony), or 2) form two sub-populations at either ephemeral water sources / open desert sites (oasis hypothesis) or at 3) burnt versus unburnt sites (wildfire hypothesis), or 4) form three sub-populations organised by shared rainfall gradients (productivity hypothesis). We used MARSS models to identify spatial structure and potential drivers, such as local rainfall, food resources, plant cover and species interactions that may influence the populations and sub-populations of the six desert species. The drivers were considered significant if the credible interval (CI; a measure of uncertainty; i.e., the effect lies with a 95% probability interval) did not cross zero. Further details

and explanations behind the generation of the above hypotheses can be found in Greenville *et al.* (2016a, b).

Study species

Two species of rodent, *Pseudomys hermannsburgensis* (sandy inland mouse; 12 g) and *Notomys alexis* (spinifex hopping mouse; 35 g), and one species of dasyurid marsupial, *Sminthopsis youngsoni* (lesser hairy-footed dunnart; 10 g), were investigated. These species were chosen to illustrate their divergent population responses to rainfall and spatial dynamics. Within arid Australia, *P. hermannsburgensis*, *N. alexis* and *S. youngsoni* occur in hummock grasslands (*Triodia* spp.). Unlike many other species of desert rodents around the world, *P. hermannsburgensis* and *N. alexis* are omnivorous, consuming a wide range of seeds, invertebrates and green plant material (Murray and Dickman 1994a; Murray and Dickman 1994b). Both species of rodent exhibit ‘booms’ and ‘busts’ in population numbers, with captures increasing up to 60-fold within six months during ‘boom’ conditions (Dickman *et al.* 2010; Dickman *et al.* 1999b). *Sminthopsis youngsoni* is an insectivorous dasyurid. It breeds in late winter or early spring when animals are aged at least 8–10 months, and independent juveniles first appear usually in summer (Dickman *et al.* 2001). This species is capable of having a second litter, but does so rarely depending on the availability of food (Dickman *et al.* 2001).

One species of skink (*Lerista labialis*) and two species of agamid (*Ctenophorus isolepis* and *Ctenophorus nuchalis*) were selected for analysis due to their different responses to environmental factors, such as rainfall and wildfire, and life history traits. *Lerista labialis* (1 g) is a fossorial, nocturnal skink that occurs mostly on dune crests (Greenville and Dickman 2009). The loose sand on the crests facilitates burrowing; populations respond positively after wildfire, presumably due to the loss of vegetation and increased sand movement (Greenville and Dickman 2009; Letnic *et al.* 2004). This skink breeds in summer and can produce more than one clutch per year if conditions are favourable (Greenville and Dickman 2005). It specialises on termites (Greenville and Dickman 2005).

Ctenophorus isolepis (6 g) and *C. nuchalis* (20 g) have predominantly annual life cycles (Dickman *et al.* 1999a). For *C. nuchalis*, capture rates are often associated with open areas and dead wood, whereas *C. isolepis* is associated with spinifex (Daly *et al.* 2007; Daly *et al.* 2008; Dickman *et al.* 1999a). Both species are insectivorous, but the diet of *C. nuchalis* includes more plant material than that of *C. isolepis* (Daly *et al.* 2008).

Field methods

We used the same grids for vertebrate sampling as for spinifex monitoring, above, using 36 pitfall traps established on each of the 12 1-ha grids set up in 1990

and 1991 on Ethabuka Station (now Ethabuka Reserve) and on the 2–5 1-ha grids set up between 1995 and 1997 at eight further sites (see Figure 2). Small vertebrates have been trapped at each site every year until the present, but here we present data only until 2012 (total 17–22 years; 130 sampling trips; 205 524 trap nights). To account for unequal trapping effort when analysing and presenting our results, live-capture counts were standardised per 100 trap nights (TN: trap nights = traps × nights opened) and averaged for each year. The characteristics of the sites, sampling methods and key results are described in detail elsewhere, with summaries in Dickman *et al.* (2014) and Greenville *et al.* (2016a, b).

Results

In total, 16 617 captures of rodents and 4586 captures of dasyurids were made over the period of study, yielding trap success rates of 8.09% and 2.23%, respectively (Greenville *et al.* 2016a). Both *P. hermannsburgensis* (7878 captures) and *N. alexis* (5146 captures) exhibited similar synchronous spatial population dynamics (Figure 3). The MARSS models showed that populations of both rodent species were affected positively by spinifex seed productivity (0.52 (CI: 0.26–0.78) and 0.40 (CI: 0.14–0.65), respectively) and annual rainfall (0.52 (CI: 0.30–0.77) and 0.55 (CI: 0.34–0.75), respectively) in the previous year. Both species also had similar process (0.51 (CI: 0.33–0.79) and 0.39 (CI: 0.24–0.61), respectively) and observation errors (0.48 (CI: 0.42–0.54) and 0.47 (CI: 0.41–0.53), respectively) indicating similarity in population dynamics and trappability. The two rodent species showed some evidence of density-dependence (Greenville *et al.* 2016a).

For *S. youngsoni* (2491 captures), the best fitting MARSS model suggested that sub-populations at all nine sites were distinct (asynchronous) and exhibited density-dependence (Figure 4) (Greenville *et al.* 2016a). There was no support for the oasis, wildfire or productivity hypotheses (Greenville *et al.* 2016a). Observation errors and process errors were similar across sub-populations for *S. youngsoni*, suggesting similar trappability (Table 1), but there were large variations in the process errors (Table 1). The effect of spinifex cover and antecedent annual rainfall were site-specific, suggesting that drivers for sub-populations of this species acted on a local scale (Figure 4) (Greenville *et al.* 2016a). The predator, *Dasyercus blythi* (brush-tailed mulgara), had a negative effect on *S. youngsoni* populations (-0.59; CI: -0.83 – -0.37).

In total, 17 681 captures of individuals of 58 species of reptiles were made over the period of study, yielding an overall trap success rate of 8.6% in relation to the total trapping effort (Greenville *et al.* 2016b). The best predicting MARSS population model for *L. labialis* (5663 captures), was the wildfire model, suggesting that populations of this species are structured into two sub-populations across the study region based on their recent

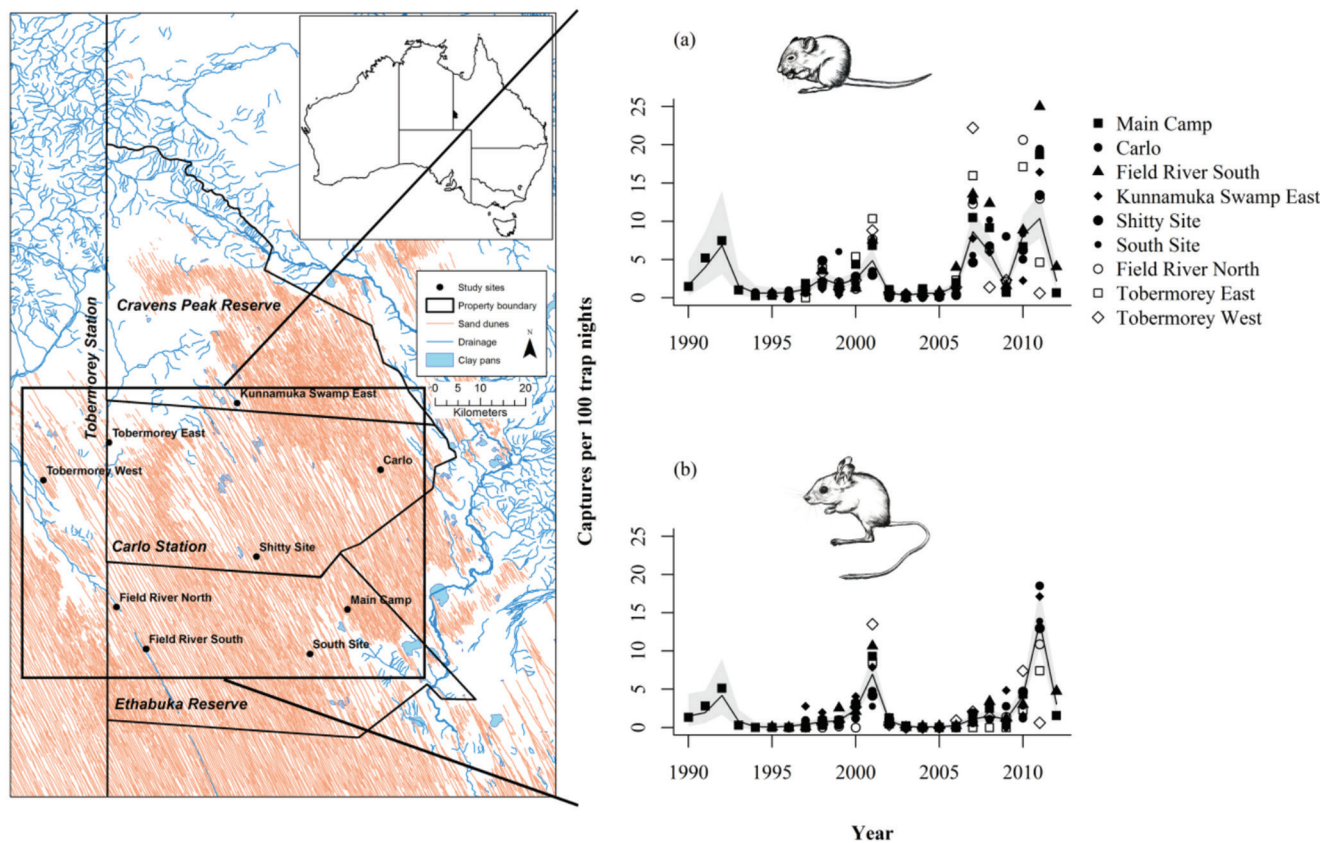


Figure 3: Predicted population sizes (lines) and captures (dots; captures/100 trap nights) predicted from MARSS models for (a) *Pseudomys hermannsburgensis*, and (b) *Notomys alexis* synchronous population models, Simpson Desert, central Australia (map). Time-series data were collected from nine sites (sub-populations) monitored 2–6 times per year for 17–22 yr (1990–2012 for one site and 1995–2012 for eight sites; 130 sampling trips). Shaded areas indicate 95% credible intervals. Illustrations by Alison Foster. Figure reproduced from Greenville et al. (2016), *Ecosphere* 7: e01343.

fire history (Figure 5). The oasis model was the best predictor for *C. isolepis* (2514 captures), suggesting that this species is structured into two sub-populations at, and away from, oases (Figure 5). In contrast, *C. nuchalis* (1303 captures) exhibited synchronous dynamics across the nine sites (Figure 5). MARSS population models showed that rainfall and spinifex cover did not influence each reptile population (Table 1). Process and observation errors were similar across all species examined (Table 1), except for the observation error for *C. nuchalis*, which was lower than for all other species (Table 1).

Discussion

MARSS models allowed us to successfully uncover different population trajectories for our desert study species. Furthermore, varied spatial dynamics were discovered, even with incomplete datasets—due to fieldwork fail moments—collected by multiple observers. Traditional regression methods (e.g., Generalised Linear Models) assume that observation error is small and consistent. However, our results suggest that observation errors were large and similar to process errors. Indeed, the observation errors for each species were similar to the environmental stochasticity in a highly dynamic environment. The MARSS models successfully partitioned both process and

observation errors in our two case studies, allowing for errors from multiple observers and changes in detectability to be accounted for in population estimates.

Observation errors were higher than process errors for spinifex cover, which may reflect the high observer error associated with rapid visual cover estimates in the field (Helm and Mead 2004; Vittoz et al. 2010). Nonetheless, the results of the MARSS models suggested that populations of spinifex were structured by wildfire. Nguyen et al. (2015) compared MARSS models using two different spinifex datasets from the same study region: one from a rapid visual assessment of cover, as above, and the other from a high-resolution plot-based cover estimate. The results from both datasets were consistent in showing that spinifex was structured into two populations by wildfire, and thus confirm that rapid visual assessment of vegetation cover can be a useful method in long-term studies if observation error is accounted for (Nguyen et al. 2015).

The MARSS models uncovered contrasting spatial dynamics between the rodent (*P. hermannsburgensis* and *N. alexis*) and dasyurid (*S. youngsoni*) species investigated. The nine sub-populations of rodents exhibited spatial synchrony in their population trajectories, whereas *S. youngsoni* showed asynchronous dynamics across space.

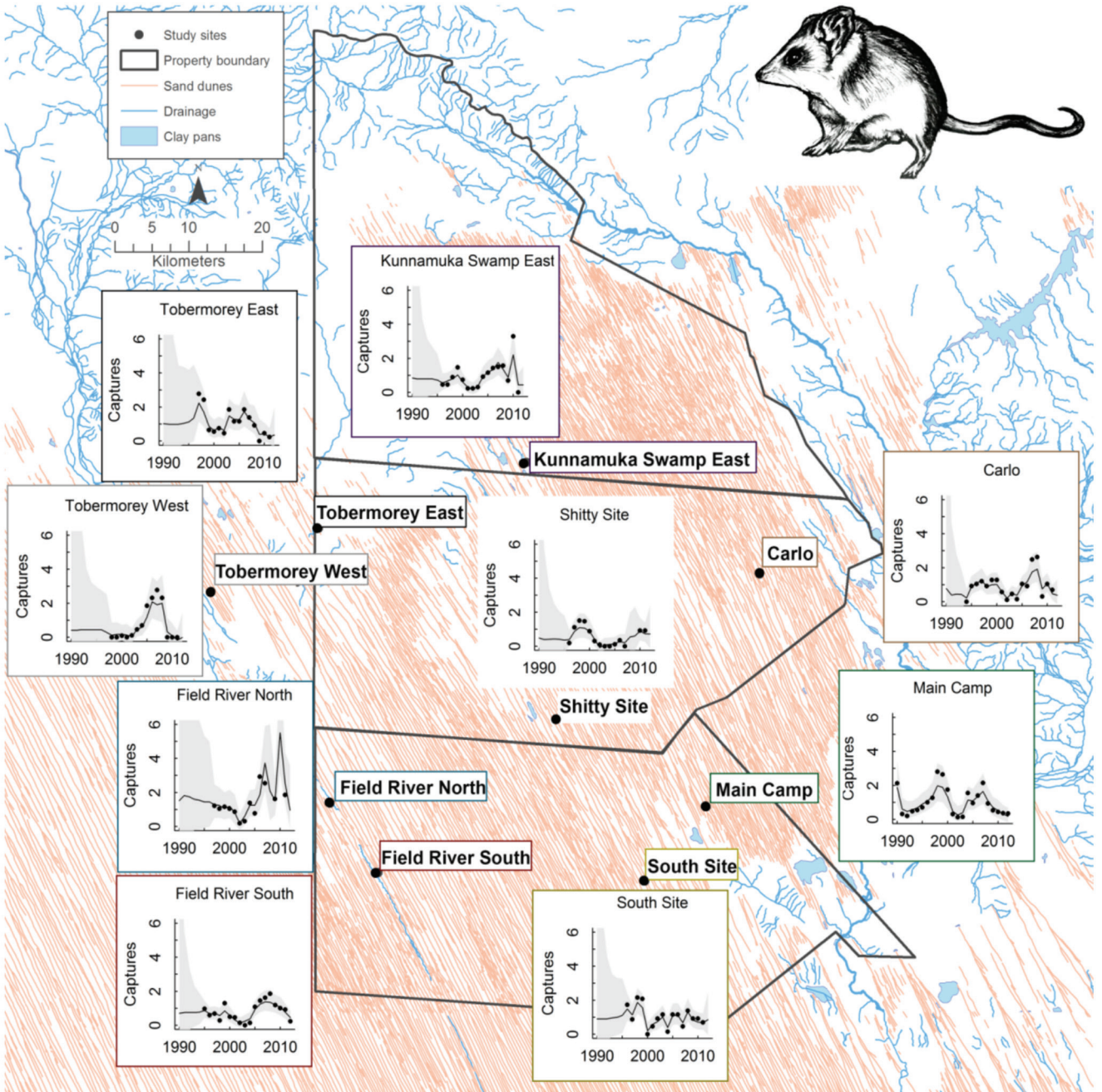


Figure 4: Predicted population sizes (lines) and captures (dots; captures/100 trap nights) from a MARSS model for *Sminthopsis youngsoni* depicting asynchronous spatial population dynamics, Simpson Desert, central Australia. Time-series data were collected from nine sites (sub-populations) monitored 2–6 times per year for 17–22 yr (1990–2012 for one site and 1995–2012 for eight sites; 130 sampling trips). Shaded areas indicate 95% credible intervals. Illustrations by Alison Foster. Figure reproduced from Greenville *et al.* (2016), *Ecosphere* 7: e01343.

Rodent populations responded positively to spinifex seed production and rainfall from the previous year. Greenville *et al.* (2016a) found that annual rainfall was highly synchronous across the study region and thus synchronises the nine rodent sub-populations. In contrast, *S. youngsoni* responded to local events, such as rainfall at some sites and spinifex cover at others. The different life histories of the rodents and the dasyurid may provide one explanation for the contrasting dynamics. The two rodent species are omnivorous (Murray and Dickman 1994a; Murray and Dickman 1994b) and can breed quickly, allowing them

to respond within six months to rainfall events (Dickman *et al.* 2010; Dickman *et al.* 1999b). *Sminthopsis youngsoni* is insectivorous and usually breeds once per year in late winter or early spring (Dickman *et al.* 2001) and thus only responds slowly to increases in productivity.

The three reptile species showed no response to rainfall or spinifex cover, but nonetheless exhibited different spatial dynamics. The wildfire hypothesis was the best supported model for *L. labialis*, whereas the oasis and population synchrony hypotheses were the best supported models for

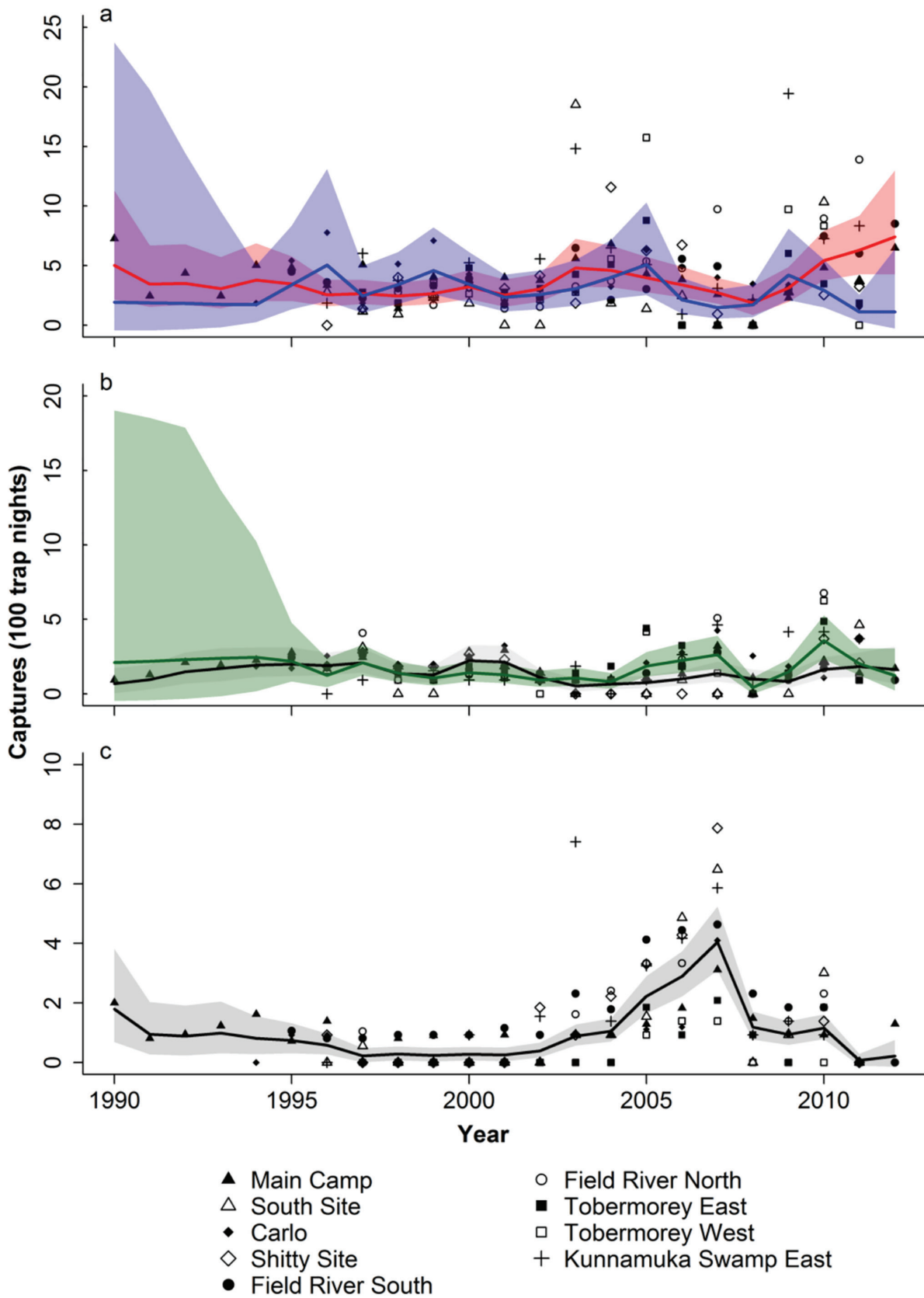


Figure 5: Predicted population size (line) and captures (dots; captures/100 trap nights) from MARSS models for wildfire population model for (a) *Lerista labialis* (burnt: red line, unburnt: blue line), (b) oasis population model for *Ctenophorus isolepis* (oasis: green line, open desert: black line) and (c) synchronous population model for *Ctenophorus nuchalis*, Simpson Desert, central Australia. Time series data were collected from nine sites (sub-populations) monitored two to six times per year for 13–22 years. Shaded areas indicate 95% credible intervals. Wildfires occurred in 1975, 2002 and 2012.

Table 1: The results of MARSS models for captures of mammals and reptiles (100 trap nights, log + 1 transformed), Simpson Desert, central Australia. There is only one observation error (r^2) element for each species, as it was assumed to be equal for each sub-population. Covariates were considered significant if the 95% credible intervals (CI) did not cross zero, and are shown in bold.

Model covariates	Rainfall	Spinifex cover	Process error (q^2)	Observation error (r^2)
<i>Sminthopsis youngsoni</i>				
Population Main Camp	-0.08 (-0.46 to 0.29)	0.10 (-0.32 to 0.52)	0.53 (0.12 to 0.99)	0.56 (0.32 to 0.75)
Carlo	-0.07 (-0.47 to 0.34)	-0.34 (-0.72 to 0.04)	0.38 (0.08 to 0.91)	
Field River South	-0.04 (-0.42 to 0.33)	0.02 (-0.38 to 0.46)	0.41 (0.09 to 0.90)	
Kunnamuka Swamp East	0.25 (-0.16 to 0.66)	-0.31 (-0.73 to 0.23)	0.33 (0.08 to 0.86)	
Shitty Site	0.28 (-0.28 to 0.83)	0.40 (-0.23 to 0.94)	0.59 (0.10 to 1.31)	
South Site	-0.10 (-0.66 to 0.43)	0.65 (-0.13 to 1.23)	0.43 (0.08 to 1.08)	
Field River North	0.59 (0.16 to 1.02)	-0.08 (-0.48 to 0.35)	0.30 (0.07 to 0.75)	
Tobermorey East	-0.44 (-1.03 to 0.19)	-0.08 (-0.73 to 0.58)	0.67 (0.13 to 1.35)	
Tobermorey West	-0.28 (-0.78 to 0.19)	-0.53 (-1.00 to -0.01)	0.28 (0.07 to 0.76)	
<i>Lerista labialis</i>				
Population (burnt)	0.17 (-0.15 to 0.48)	-0.08 (-0.38 to 0.18)	0.49 (0.20 to 0.93)	0.83 (0.72 to 0.95)
Population (unburnt)	-0.41 (-0.94 to 0.05)	-0.05 (-0.46 to 0.35)	0.65 (0.19 to 1.24)	
<i>Ctenophorus isolepis</i>				
Population (Oasis)	0.29 (-0.05 to 0.64)	-0.01 (-0.30 to 0.30)	0.54 (0.23 to 0.91)	0.75 (0.66 to 0.87)
Population (Open desert)	0.19 (-0.34 to 0.71)	-0.10 (-0.61 to 0.42)	0.96 (0.51 to 1.57)	
<i>Ctenophorus nuchalis</i>				
Population (synchronous)	-0.13 (-0.44 to 0.20)	0.01 (-0.29 to 0.32)	0.63 (0.42 to 0.93)	0.56 (0.49 to 0.63)

C. isolepis and *C. nuchalis*, respectively. Thus there was little evidence that rainfall drove population synchrony for the three reptile species, but their populations were structured in space into one or two sub-populations by other landscape-scale factors, such as wildfire and ephemeral areas of higher productivity. *Lerista labialis* may respond to changes in termite abundance and removal of vegetation after wildfire (Letnic *et al.* 2004). Loose sand allows easier movement for this termite specialist and greater access to foraging areas (Greenville and Dickman 2005; Greenville and Dickman 2009). *Ctenophorus isolepis* has a predominantly annual life cycle and thus may have greater reproduction success and survival at oasis sites (ephemeral water courses) compared to drier open desert locations. The synchronous dynamics exhibited by *C. nuchalis* suggest that a landscape-scale driver is operating, but that driver clearly is not rainfall or spinifex cover. *Ctenophorus nuchalis* exhibits a marked preference for open areas, even though open habitats may also expose it to high predation risk, particularly from birds (Daly *et al.* 2008). Predation pressure from such widely-roaming predators drive prey population synchrony in other systems (Ims and Andreassen 2000), and it is possible that predation also may synchronise populations of *C. nuchalis* here.

Implications for management

The MARSS modelling approach showed that our study species responded in different ways to drivers such as wildfire and rainfall, and also exhibited contrasting spatial population dynamics across the nine study sites. These results highlight that a single management approach for arid zone species would be inappropriate, and likely applicable only to a subset of taxa. Although many arid-zone species respond to rainfall (Ward 2016; Whitford 2002), this study shows that the timing, location and scale of response can vary greatly. Thus, drawing simple trend lines for populations may not uncover the true complexity of how species respond to environmental change (Dickman *et al.* 2018).

More broadly, this study also highlights the role that long-term monitoring can play in the conservation of species and ecological systems. Long-term studies that monitor populations, population drivers or environmental variables at multiple sites across decades and use modern statistical approaches allow us to gain a particularly deep understanding of how ecosystems operate and respond to environmental change (Lindenmayer *et al.* 2014). The drivers that we monitored and the hypotheses

that were tested in this study were only possible by first understanding the individual biology of each species. Unfortunately, such studies—especially those focussed on individual species or even groups of species—are under threat by diminishing research funding and promotion pressures to study global questions.

Future applications

In addition to analysing multiple populations of single species, MARSS models can also be used to combine data from multiple time-series datasets in different ways (Holmes *et al.* 2014). Firstly, data that are collected using different methods to estimate the same population index can be combined. This is possible by assigning different observation errors for the different methods; that is, one can test if the same population process is being measured by the two or more methods (Holmes *et al.* 2014). For example, one can combine population estimates from aerial and ground counts of water birds, which may have occurred across different time-periods. Secondly, state-space models are used extensively in tracking studies to investigate animal movements. MARSS models can be used to combine multiple animal or species tracking datasets to investigate large-scale movements of species and interactions in space from multiple species or individuals. Thirdly, MARSS models can be used to investigate species interactions, such as the interaction between predator and prey, competition or full food webs. For example, Greenville *et al.* (2016a) found that the carnivorous mulgara, *Dasyercus blythi*, had a negative effect on *S. youngsoni*, but a positive influence on populations of *Ningauai ridei*. The mulgara may act as a keystone species; when present it suppresses the abundance of *S. youngsoni* to the benefit of the smaller *N. ridei* (Dickman 2003). Walsh *et al.* (2016)

used MARSS modelling to estimate the economic impacts of invasive species that cascade through the Lake Mendota (Wisconsin) food web. Using multiple long-term time-series data, these authors estimated the economic damage arising from the degradation of ecosystem services by invasive species to be US\$86–US\$163 million over a 20 year period. Lastly, MARSS models were able to handle up to nine years of missing surveys from some sites in our studies. However, further research is required to fully understand how many missing values and how they are distributed throughout the time-series affect model performance.

Conclusion

MARSS models are a useful tool for interrogating time-series data collected in long-term monitoring programs. Not only can these models incorporate both observation and process errors, they can also incorporate missing values that often arise from problems that occur in the field. By simultaneously analysing multiple sub-populations of species, and their putative drivers, complex spatial dynamics can be revealed. Our case studies from central Australia showed that species responded to different environmental drivers that operated at local to landscape-scales. Species that responded at the landscape-scale were often driven by rainfall or wildfire, but there were no similarities within families. Life history traits were more useful in explaining dynamics, illustrating that long-term monitoring, along with studies that elucidate the basic biology of species, are required to develop a deep understanding of how ecosystems function. Targeted management strategies can only then be developed to identify and reverse declines in species populations or ecological systems.

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References

- Ahrestani, F. S., Hebblewhite, M., Post, E. 2013. The importance of observation versus process error in analyses of global ungulate populations. *Sci. Rep.* 3: 3125. <http://dx.doi.org/10.1038/srep03125>
- Allan, G., Southgate, R. 2002. Fire regimes in the spinifex landscapes of Australia. Pp. 145-176 in *Flammable Australia: the fire regimes and biodiversity of a continent*. edited by R. A. Bradstock, J. E. Williams and A. M. Gill. Cambridge University Press: Cambridge
- Berryman, A., Turchin, P. 2001. Identifying the density-dependent structure underlying ecological time series. *Oikos* 92: 265-270. <http://dx.doi.org/10.1034/j.1600-0706.2001.920208.x>
- Berryman, A. A. 1999. *Principles of Population Dynamics and Their Application*. Stanley Thornes, UK
- Bjørnstad, O. N., Ims, R. A., Lambin, X. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution* 14: 427-432. [http://dx.doi.org/10.1016/s0169-5347\(99\)01677-8](http://dx.doi.org/10.1016/s0169-5347(99)01677-8)
- Blackwell, G. L., Bassett, S. M., Dickman, C. R. 2006. Measurement error associated with external measurements commonly used in small-mammal studies. *Journal of Mammalogy* 87: 216-223. <http://dx.doi.org/doi:10.1644/05-MAMM-A-215R1.1>
- Boehmke, B. C. 2016. Dealing with missing values. Pp. 113-116 in *Data Wrangling with R*. edited by Springer International Publishing: Cham. http://dx.doi.org/10.1007/978-3-319-45599-0_14
- Braswell, B. H., Schimel, D. S., Linder, E., Moore, B. 1997. The response of global terrestrial ecosystems to interannual emperature variability. *Science* 278: 870-873. <http://dx.doi.org/10.1126/science.278.5339.870>
- Daly, B. G., Dickman, C. R., Crowther, M. S. 2007. Selection of habitat components by two species of agamid lizards in sandridge desert, central Australia. *Austral Ecology* 32: 825-833. <http://dx.doi.org/DOI 10.1111/j.1442-9993.2007.01768.x>
- Daly, B. G., Dickman, C. R., Crowther, M. S. 2008. Causes of habitat divergence in two species of agamid lizards in arid central Australia. *Ecology* 89: 65-76
- Dickman, C., Wardle, G. M., Foulkes, J., de Preu, N. 2014. Desert complex environments. Pp. 379-438 in *Biodiversity and environmental change: monitoring, challenges and direction*. edited by D. Lindenmayer, E. Burns, N. Y. Thurgate and A. Lowe. CSIRO Publishing: Melbourne
- Dickman, C. R. 2003. Species interactions: indirect effects. Pp. 158-170 in *Ecology: an Australian perspective*. edited by P. Attiwill and B. Wilson. Oxford University Press: Melbourne.
- Dickman, C. R., Greenville, A. C., Beh, C.-L., Tamayo, B., Wardle, G. M. 2010. Social organization and movements of desert rodents during population “booms” and “busts” in central Australia. *Journal of Mammalogy* 91: 798-810. <http://dx.doi.org/10.1644/09-mamm-s-205.1>
- Dickman, C. R., Greenville, A. C., Wardle, G. M. 2018. Determining trends in irruptive desert species. Pp. 281-292 in *Monitoring threatened species and ecological communities*. edited by S. Legge, D. B. Lindenmayer, N. Robinson, B. Scheele, D. M. Southwell and B. Wintle. CSIRO Publishing: Melbourne
- 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. *Wildlife Research* 28: 493-506
- Dickman, C. R., Letnic, M., Mahon, P. S. 1999a. Population dynamics of two species of dragon lizards in arid Australia: the effects of rainfall. *Oecologia* 119: 357-366
- Dickman, C. R., Mahon, P. S., Masters, P., Gibson, D. F. 1999b. Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildlife Research* 26: 389-403
- Eckhardt, H. C., van Wilgen, B. W., Biggs, H. C. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology* 38: 108-115. <http://dx.doi.org/10.1046/j.1365-2028.2000.00217.x>
- Greenville, A. C., Dickman, C. R. 2005. The ecology of *Lerista labialis* (Scincidae) in the Simpson Desert: reproduction and diet. *Journal of Arid Environments* 60: 611-625
- Greenville, A. C., Dickman, C. R. 2009. Factors affecting habitat selection in a specialist fossorial skink. *Biological Journal of the Linnean Society* 97: 531-544. <http://dx.doi.org/10.1111/j.1095-8312.2009.01241.x>
- Greenville, A. C., Dickman, C. R., Wardle, G. M., Letnic, M. 2009. The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. *International Journal of Wildland Fire* 18: 631-639. <http://dx.doi.org/10.1071/WF08093>
- Greenville, A. C., Wardle, G. M., Nguyen, V., Dickman, C. R. 2016a. Population dynamics of desert mammals: similarities and contrasts within a multispecies assemblage. *Ecosphere* 7: e01343. <http://dx.doi.org/10.1002/ecs2.1343>
- Greenville, A. C., Wardle, G. M., Nguyen, V., Dickman, C. R. 2016b. Spatial and temporal synchrony in reptile population dynamics in variable environments. *Oecologia* 182: 475-85. <http://dx.doi.org/10.1007/s00442-016-3672-8>
- Hannaford, M. J., Barbour, M. T., Resh, V. H. 1997. Training Reduces Observer Variability in Visual-Based Assessments of Stream Habitat. *Journal of the North American Benthological Society* 16: 853-860. <http://dx.doi.org/doi:10.2307/1468176>

- 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. <http://dx.doi.org/10.1111/j.2006.0906-7590.04307.x>
- Heino, M., Kaitala, V., Ranta, E., Lindström, J. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society of London B: Biological Sciences* 264: 481-486
- Helm, D. J., Mead, B. R. 2004. Reproducibility of vegetation cover estimates in south-central Alaska forests. *Journal of Vegetation Science* 15: 33-40. <http://dx.doi.org/DOI 10.1111/j.1654-1103.2004.tb02234.x>
- Hinrichsen, R. A., Holmes, E. E. 2009. Using multivariate state-space models to study spatial structure and dynamics. Pp. 1-20 in *Spatial Ecology*. edited by R. S. Cantrell, C. Cosner and S. Ruan. CRC/Chapman Hall: London
- Holmes, E., Ward, E., Wills, K. 2013. MARSS: multivariate autoregressive state-space modeling. R package version 3.4.
- Holmes, E. E., Ward, E. J., Scheuerell, M. D. 2014. *Analysis of multivariate time-series using the MARSS package*. NOAA Fisheries: Seattle, USA.
- Holmes, E. E., Ward, E. J., Wills, K. 2012. MARSS: multivariate autoregressive state-space models for analyzing time-series data. *R Journal* 4: 11-19
- Hutchinson, C. E. 1984. The Kalman filter applied to aerospace and electronic systems. *IEEE Transactions on Aerospace and Electronic Systems* AES-20: 500-504. <http://dx.doi.org/10.1109/TAES.1984.4502068>
- Ims, R. A., Andreassen, H. P. 2000. Spatial synchronization of vole population dynamics by predatory birds. *Nature* 408: 194-196
- Joffe, R., Rambal, S. 1993. How tree cover influences the water balance of Mediterranean rangelands. *Ecology* 74: 570-582. <http://dx.doi.org/10.2307/1939317>
- 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. *Journal of Arid Environments* 59: 85-114. <http://dx.doi.org/DOI 10.1016/j.jaridenv.2004.01.014>
- Lindgren, M., Mollmann, C., Nielsen, A., Stenseth, N. C. 2009. Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *Proceedings of the National Academy of Sciences of the United States of America* 106: 14722-7. <http://dx.doi.org/10.1073/pnas.0906620106>
- Lindenmayer, D. In press. Why is long-term ecological research and monitoring so hard to do? (And what can be done about it). *Australian Zoologist*. <http://dx.doi.org/10.7882/az.2017.018>
- Lindenmayer, D., Burns, E., Thurgate, N. Y., Lowe, A. (Eds) (2014). 'Biodiversity and environmental change : monitoring, challenges and direction.' (CSIRO Publishing: Melbourne)
- Lindenmayer, D., Burns, E. L., et al. 2017. Save Australia's ecological research. *Science* 357: 557-557. <http://dx.doi.org/10.1126/science.aao4228>
- Lindenmayer, D. B., Likens, G. E., et al. 2012. Value of long-term ecological studies. *Austral Ecology* 37: 745-757. <http://dx.doi.org/10.1111/j.1442-9993.2011.02351.x>
- Morellet, N., Gaillard, J.-M., Hewison, A. J. M., Ballon, P., Boscardin, Y., Duncan, P., Klein, E., Maillard, D. 2007. Indicators of ecological change: new tools for managing populations of large herbivores. *Journal of Applied Ecology* 44: 634-643. <http://dx.doi.org/10.1111/j.1365-2664.2007.01307.x>
- Murray, B. R., Dickman, C. R. 1994a. Food preferences and seed selection in two species of Australian desert rodent. *Wildlife Research* 21: 647-655. <http://dx.doi.org/http://dx.doi.org/10.1071/WR9940647>
- Murray, B. R., Dickman, C. R. 1994b. Granivory and microhabitat use in Australian desert rodents: are seeds important? *Oecologia* 99: 216-225. <http://dx.doi.org/10.1007/bf00627733>
- Nakagawa, S., Freckleton, R. P. 2008. Missing inaction: the dangers of ignoring missing data. *Trends in Ecology & Evolution* 23: 592-596. <http://dx.doi.org/http://dx.doi.org/10.1016/j.tree.2008.06.014>
- Nano, C. E., Clarke, P., Pavey, C. R. 2012. Fire regimes in arid hummock grasslands and Acacia shrublands. Pp. 195-214 in *Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world.*, edited by R. A. Bradstock, A. M. Gill and R. J. Williams. CSIRO Publishing: Melbourne
- Newman, K., Buckland, S. T., Morgan, B., King, R., Borchers, D. L., Cole, D., Besbeas, P., Gimenez, O., Thomas, L. 2014. *Modelling population dynamics : model formulation, fitting and assessment using state-space methods*. Springer: New York.
- Nguyen, V., Greenville, A. C., Dickman, C. R., Wardle, G. M. 2015. On the validity of visual cover estimates for time series analyses: a case study of hummock grasslands. *Plant Ecology* 216: 975-988. <http://dx.doi.org/10.1007/s11258-015-0483-7>
- Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J. 2008. State-space models of individual animal movement. *Trends in Ecology & Evolution* 23: 87-94. <http://dx.doi.org/http://dx.doi.org/10.1016/j.tree.2007.10.009>
- Plummer, M. 2013. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. version 4.2.0
- Plummer, M. 2014. rjags: Bayesian graphical models using MCMC. R package version 3-13.

- R Core Team.** 2017. R: a language and environment for statistical computing.
- Royle, J. A., Dorazio, R. M.** 2008. *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Academic Press: New York.
- Shaw, C.** 2015. Scientists share their embarrassing #fieldworkfail stories The Guardian.
- Su, Y.-S., Yajima, M.** 2014. R2jags: a package for running jags from R. R package version 0.04-03.
- Thompson, A. A., Mapstone, B. D.** 1997. Observer effects and training in underwater visual surveys of reef fishes. *Marine Ecology Progress Series* 154: 53-63
- Van Noorden, R., Brumfiel, G.** 2010. Fixing a grant system in crisis. *Nature News* 464: 474-475
- Vicente-Serrano, S. M., Lasanta, T., Romo, A.** 2004. Analysis of spatial and temporal evolution of vegetation cover in the Spanish Central Pyrenees: role of human management. *Environmental Management* 34: 802-818. <http://dx.doi.org/10.1007/s00267-003-0022-5>
- Vittoz, P., Bayfield, N., Brooker, R., Elston, D. A., Duff, E. I., Theurillat, J.-P., Guisan, A.** 2010. Reproducibility of species lists, visual cover estimates and frequency methods for recording high-mountain vegetation. *Journal of Vegetation Science* 21: 1035-1047. <http://dx.doi.org/10.1111/j.1654-1103.2010.01216.x>
- Walsh, J. R., Carpenter, S. R., Vander Zanden, M. J.** 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *Proceedings of the National Academy of Sciences* 113: 4081-4085. <http://dx.doi.org/10.1073/pnas.1600366113>
- Ward, D.** 2016. *The biology of deserts*. Second edition. edn. Oxford University Press: Oxford.
- Ward, E. J., Chirakkal, H., González-Suárez, M., Aurióles-Gamboa, D., Holmes, E. E., Gerber, L.** 2010. Inferring spatial structure from time-series data: using multivariate state-space models to detect metapopulation structure of California sea lions in the Gulf of California, Mexico. *Journal of Applied Ecology* 47: 47-56. <http://dx.doi.org/10.1111/j.1365-2664.2009.01745.x>
- Wardle, G. M., Nano, C.** 2017. Hummock grasslands: *Triodia*-dominated grasslands in arid Australia. in *Australian Vegetation*. Third Edition edn, edited by D. Keith. CSIRO Publishing: Melbourne
- Wardle, G. M., Pavey, C. R., Dickman, C. R.** 2013. Greening of arid Australia: New insights from extreme years. *Austral Ecology* 38: 731-740. <http://dx.doi.org/10.1111/aec.12073>
- Westoby, M., Rice, B., Griffin, G., Friedel, M.** 1988. The soil seed bank of *Triodia basedowii* in relation to time since fire. *Austral Ecology* 13: 161-169. <http://dx.doi.org/doi:10.1111/j.1442-9993.1988.tb00965.x>
- Whitford, W. G.** 2002. *Ecology of desert systems*. Academic Press: London.
- Winkworth, R.** 1967. The composition of several arid spinifex grasslands of central Australia in relation to rainfall, soil water relations, and nutrients. *Australian Journal of Botany* 15: 107-130. <http://dx.doi.org/http://dx.doi.org/10.1071/BT9670107>
- Wright, B. R., Zuur, A. F., Chan, G. C. K.** 2014. Proximate causes and possible adaptive functions of mast seeding and barren flower shows in spinifex grasses (*Triodia* spp.) in arid regions of Australia. *The Rangeland Journal* 36: 297-308. <http://dx.doi.org/http://dx.doi.org/10.1071/RJ13104>