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POPULATION ECOLOGY – ORIGINAL RESEARCH

Spatial and temporal synchrony in reptile population dynamics in variable environments

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Abstract Resources are seldom distributed equally across space, but many species exhibit spatially synchronous population dynamics. Such synchrony suggests the operation of large-scale external drivers, such as rainfall or wildfire, or the influence of oasis sites that provide water, shelter, or other resources. However, testing the generality of these factors is not easy, especially in variable environments. Using a long-term dataset (13–22 years) from a large (8000 km^2) study region in arid Central Australia, we tested firstly for regional synchrony in annual rainfall and the dynamics of six reptile species across nine widely separated sites. For species that showed synchronous spatial dynamics, we then used multivariate follow a multivariate auto-regressive state–space (MARSS) models to predict that regional rainfall would be positively associated with their populations. For asynchronous species, we used MARSS models to explore four other possible population structures: (1) populations were asynchronous, (2) differed between oasis and non-oasis sites, (3) differed between burnt and unburnt sites, or (4) differed between three sub-regions with different rainfall gradients. Only one species showed evidence of spatial population synchrony and our results provide little evidence that rainfall synchronizes reptile populations. The oasis or the wildfire hypotheses were the best-fitting models for the other five species. Thus, our six study species appear generally to be structured in space into one or two populations across the study region. Our findings suggest that for arid-dwelling reptile populations, spatial and temporal dynamics are structured by abiotic events, but individual responses to covariates at smaller spatial scales are complex and poorly understood.

Keywords Population dynamics · Simpson Desert · Population structure · Moran's theorem · Wildfire

Introduction

Determining the factors that influence the spatial dynamics of species' populations remains a key goal in ecology and is imperative for managing species that are in decline. Populations across species' ranges seldom share the same level of resources and this may lead to different densities and growth rates among them (Ranta et al. 2006). Dispersal of individuals between sub-populations can dampen the independence of these units, but this effect decreases with distance (Ranta et al. 1995). However, local populations can still behave synchronously across large (>1000 km^2) areas (Ranta et al. 2006), depending on the taxon, and this behaviour suggests that large-scale drivers are operating.

Synchrony occurs in many taxa, including terrestrial mammals, birds, fish, insects and plants (Moran 1953; Hanski and Woiwod 1993; Myers 1998; Koenig and Knops 2000; Post and Forchhammer 2002; Cattanéo et al. 2003; Cattadori et al. 2005). Drivers that produce synchrony may

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include predation (Ims and Andreassen 2000), the Moran effect, which states that sub-populations with a common density-dependent structure can be synchronized by a spatially correlated density-independent factor, such as climate (Moran 1953; Bjørnstad et al. 1999), or a combination of the Moran effect and dispersal (Kendall et al. 2000; Ranta et al. 2006). In arid regions, for example, synchrony may be imposed by regional-scale sequences of droughts and flooding rains that affect all populations similarly; the synchronous 'boom' and 'bust' dynamics of desert plants and rodents exemplify this pattern (Dickman et al. 1999b; Greenville et al. 2013). However, populations may also experience varied conditions in different parts of species' ranges or show contrasting responses, even within the same family (Read et al. 2012; Greenville et al. 2016). For example, populations in different rainfall zones will likely experience different levels of productivity (Ahumada et al. 2004; Woodman et al. 2006), while populations that experience a disturbance event, such as wildfire (Letnic et al. 2004; Evans et al. 2010; Masters and Dickman 2012; Nimmo et al. 2012), may have different trajectories to those that have not been disturbed. Species that exploit patchy resources, such as ephemeral waters or oasis sites in arid regions, may also exhibit different dynamics due to elevated shelter, food or water resources at these sites (Kok and Nel 1996; Morton et al. 2011; Free et al. 2013), with populations acting as spatially independent units (Dickman et al. 2011). Moran's effect thus may be weak in highly variable environments.

Here, we test the Moran effect using Australian desert lizards. Although climatic variables often show higher levels of spatial correlation over larger distances in Australia than elsewhere (Koenig 2002), rainfall in arid Australia is highly variable in time and space (Van Etten 2009). Rainfall influences the population size, breeding and body condition of many species of lizards, in particular annual species (Dickman et al. 1999a). Presumably, rainfall increases food resources (Dickman et al. 1999a; Greenville and Dickman 2005; Schlesinger et al. 2011; Read et al. 2012) and provision of foraging and shelter sites (Daly et al. 2007, 2008). Rainfall-stimulated productivity also generates ground fuel for subsequent wildfires, and different species of lizards then enter the assemblage as vegetation regrows over time (Letnic et al. 2004; Pianka and Goodyear 2012; Smith et al. 2013). However, rainfall has little effect on lizard dispersal; animals remain sedentary for long periods (Dickman et al. 1999a). The use of lizards in highly variable desert conditions therefore provides a unique opportunity to test the generality of the Moran effect.

Using long-term population data on six species of reptiles at nine widely separated desert sites, we first test the hypothesis that annual rainfall drives regional synchrony in population dynamics. For species that do not exhibit synchrony, we then explore whether populations of these reptiles are asynchronous, form two populations at ephemeral water sources versus open desert sites (oasis hypothesis) or at burnt versus unburnt sites (wildfire hypothesis), or form three populations that are organized by shared rainfall gradients (productivity hypothesis). We use multivariate state–space models to identify potential drivers, such as local rainfall and plant cover, which may influence the populations of the six reptile species, and make the following predictions. Firstly, using Moran's theorem, we predict that the spatial correlation between the regional populations will be equal to that between the local density-independent conditions (annual rainfall). Secondly, for species with synchronous spatial dynamics, we use multivariate state–space models to predict that rainfall, operating at the landscape scale (8000 km^2), will be positively associated with their populations, whereas species with asynchronous populations will be influenced largely by factors operating at local scales. Lastly, we predict that reptile spatial population structure will be influenced by species' habitat preferences and traits, such as annual life cycles and preferences for sites with plant cover. Species associated with plant cover will be structured into two populations by wildfire (burnt and unburnt) and annual species will exhibit high levels of population synchrony due to rainfall.

Materials and methods

Study region

The study was carried out in the Simpson Desert, Central Australia (Fig. 1). This region occupies 170,000 km^2; dune fields comprise 73 % of the region, with smaller areas consisting of clay pans, rocky outcrops and gibber flats (Shephard 1992). The sand dunes run parallel in a north–south direction aligned with the prevailing southerly wind, are up to 10 m high, and spaced 0.6–1 km apart (Purdie 1984). Vegetation in the interdune swales and on dune sides is predominantly spinifex (*Triodia basedowii*) grassland with small stands of gidgee trees (*Acacia georginae*) and other woody *Acacia* shrubs or mallee eucalypts (Wardle et al. 2015); low-lying clay pans fill with water temporarily after heavy rain.

During summer, daily temperatures usually exceed 40 °C and minima in winter often fall below 5 °C (Purdie 1984). The highest rainfall occurs in summer, but heavy rains can fall locally or regionally throughout the year. Long-term weather stations in the study region are at Glenormiston (1890–2011), Boulia (1888–2011) and Birdsville (1954–2011), and have median annual rainfalls of 186 mm ($n = 121$ years), 216.2 mm ($n = 123$ years), and 153.1 mm ($n = 57$ years), respectively (Bureau of

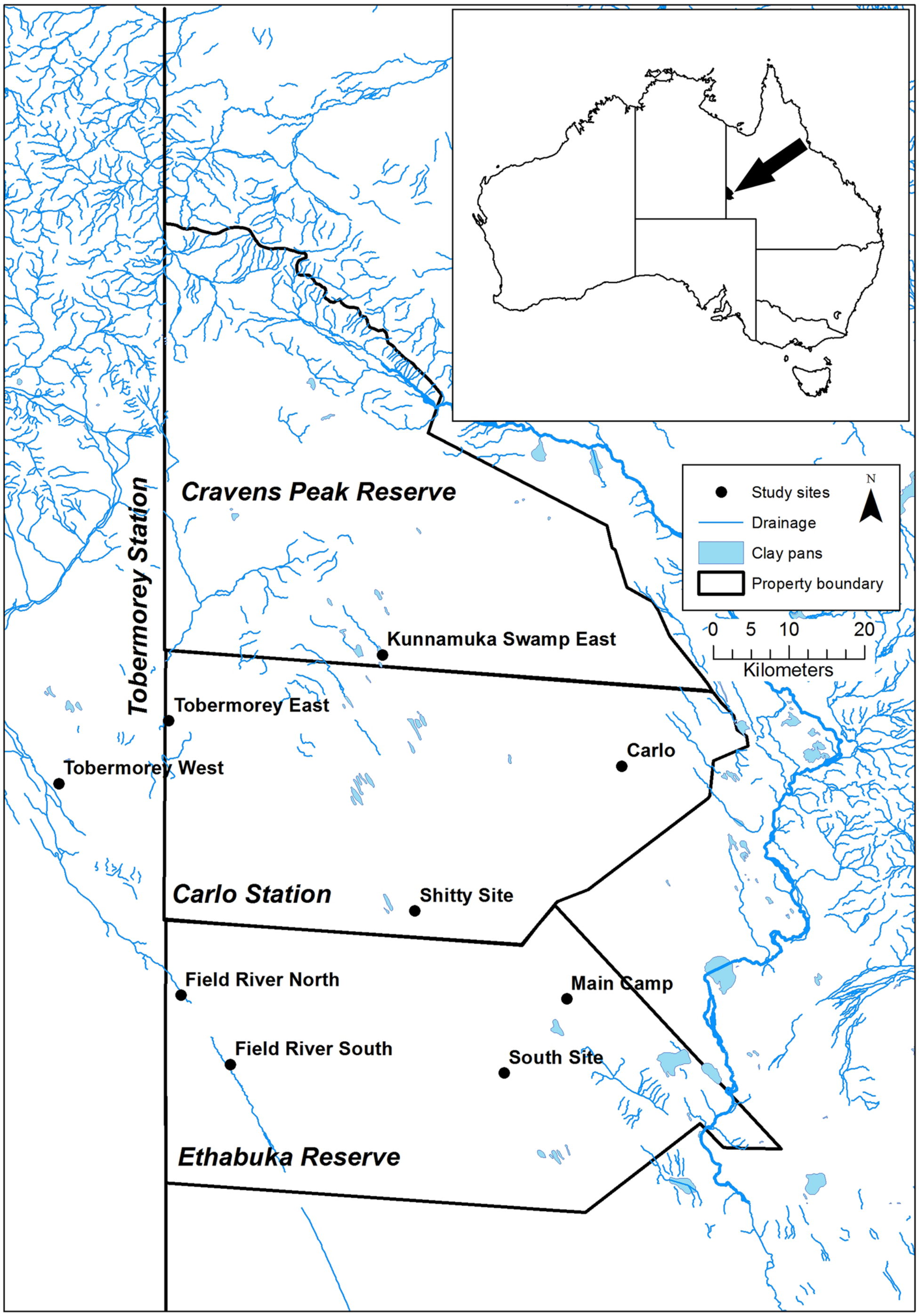

Fig. 1 Location of study sites across Cravens Peak Reserve, Carlo Station, Tobermorey Station and Ethabuka Reserve, Simpson Desert, Australia. Insert with *arrow* shows location of study region in Australia

Meteorology 2012). In general, higher rainfall is experienced in the north of the study region than in the south, and there is a weak rainfall gradient from east to west (Bureau of Meteorology 2012).

Reptiles and sampling regime

Live trapping was carried out at nine sites across Carlo Station, Tobermorey Station, Cravens Peak and Ethabuka Reserves, an 8000 km^2 desert region in south-western Queensland (Fig. 1). The nine sites were spaced >20 km apart to minimize any influence of dispersal for the small (<125 g) study species. Reptiles were live trapped using pitfall traps (16 cm diameter, 60 cm deep), each equipped with a 5 m drift fence of aluminium flywire to increase trap efficiency (Friend et al. 1989). Pitfalls were arranged on grids comprising six lines of six traps spaced 20 m apart to cover 1 ha (i.e., 36 pitfall traps per grid). The top line of the traps was positioned on a dune crest and the bottom line 100 m distant in the swale, so that each grid sampled the topography of the dune field. Sites contained 2–12 grids, and grids within sites were set 0.5–2 km apart in randomly chosen positions.

Traps were opened from 1990 to 2012 at one site (Main Camp), two to six times a year and from 1995 to 2012 at eight more sites (Shitty Site, Field River South, Field River North, South Site, Kunnamuka Swamp East, Carlo, Tobermorey East and Tobermorey West). Each trapping grid was opened for two to six nights. Data from 1990 to 1994 for one site (Main Camp) were included in the models because a large (>400 mm) rainfall event occurred in 1991, which likely influenced the population dynamics of the reptile species (Dickman et al. 1999a). The other eight sites were set up 5 years later as the project expanded. In total, Main Camp had 22 years of observations; Carlo and Field River South had 17; Kunnamuka Swamp East, Shitty Site and South Site had 15; and Field River North and Tobermorey West had 13 years of observations. Recaptures were removed from live trapping records here to avoid double counting, but the recapture rate was too low (2 % of total captures) to estimate detection probabilities (see modelling approach below). To account for unequal trapping effort, live-capture counts were standardized per 100 trap nights (TN: trap nights = traps × nights opened) and averaged per year. Not all sites were opened every year, but were included in the time series as missing values. Live-trapping data were log-transformed (log + 1) as the population models used below are in log space.

Long-term (13–22 years) live trapping (205,524 trap nights) yielded 58 species of reptiles (see Greenville 2015). Of these, only the skinks *Ctenotus pantherinus*, *C. ariadnae*, *C. dux* and *Lerista labialis*, and the dragons *Ctenophorus isolepis* and *C. nuchalis*, had sufficient data in terms of length of time series (>10 years) and captures across sites (>4 sites) to run the population models below (Table S1). These species use a wide range of habitats and have varied diets and activity patterns (Table S1) that are suitable for testing our hypotheses (Appendix S1). Species such as *C. pantherinus* and *C. ariadnae* are associated with high spinifex cover, while *C. dux* is found on open sand dunes; diets range from specialist (*C. pantherinus*) to generalist ground-invertebrate feeders (*C. ariadnae* and *C. dux*) (Downey and Dickman 1993; Haynes 1996; Gordon et al. 2010). *Lerista labialis* is a fossorial skink that specializes on termites (Greenville and Dickman 2005, 2009). *Ctenophorus isolepis* and *C. nuchalis* are annual species whose reproductive success is influenced by rainfall and spinifex cover (Dickman et al. 1999a).

Wildfire

Large-scale wildfires (>1000 km^2) have occurred three times (in 1975, 2002 and 2012) in the study region since 1972, and the mean wildfire return interval for the region is 26 years (Greenville et al. 2009; NAFI 2013). To investigate whether wildfire affected the trajectory of sub-populations of the study species, the wildfire history at the site of each sub-population was classified according to whether it had experienced a wildfire (six sites were classified as burnt, see Appendix S1) or remained unburnt (three sites were classified as unburnt, Appendix S1) across the 22-year study period.

Rainfall

Daily data from automatic weather stations (Environdata, Warwick, Queensland) at each site (Fig. S1) were used to calculate the total annual (calendar year) rainfall antecedent to capture. Weather stations were active from 1995 to 2012. To obtain rainfall data pre-1995 for Main Camp, where trapping started in 1990, we averaged annual rainfall records from the closest weather stations at Glenormiston, Sandringham, Boulia, Bedourie and Birdsville (Bureau of Meteorology 2012). The 1-year lag was used to account for the time required for fauna to respond, via breeding, to a rainfall event (Greenville et al. 2012).

Spinifex cover

To measure the cover of the dominant vegetation, spinifex, we scored ground cover visually as a percentage in 2.5 m radius plots around six traps on each reptile-trapping grid. Estimates of cover were pooled for each site, per year, over 13–22 years for each of the nine sites.

Measures of synchrony

To measure the degree of regional synchrony in reptile populations and annual rainfall at each site, we calculated the zero-lag cross-correlation for the abundance (log) for each species across the nine sites, with 1000 resamples. In addition, to investigate if the cross-correlation varied over distance between populations, we calculated the spatial cross-correlations for the abundance (log) for each species and annual rainfall (mm). The mean cross-correlation and spatial cross-correlation coefficients were calculated using the ncf 1.1-5 package (Bjornstad 2013), in R 3.02 (R Core Team 2014). If regional synchrony was found, a synchronous (1-state) autoregressive state–space population model was used to identify potential population drivers (see below). If there was little evidence for population synchrony, the population structures, and their potential drivers, were investigated using the multivariate autoregressive state–space models described below.

Bayesian multivariate autoregressive state–space models

We used Bayesian multivariate autoregressive state–space (MARSS) models to analyse live-trapping data from our nine sites and identify potential population drivers (rainfall and spinifex cover). We based the MARSS models on the Gompertz population growth model and assumed that population growth rate varies exponentially with population size and that meta-populations are closed to immigration and emigration, within the 8000 km^2 study region (Hinrichsen and Holmes 2009). The MARSS framework is hierarchical and allows modelling of different spatial population structures and parameters, 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). The MARSS framework has proven useful for modelling population data in the present study system, particularly for incorporating observation error in long-term monitoring data (Nguyen et al. 2015; Greenville et al. 2016).The process component is a multivariate first-order autoregressive process and is written in log space (Holmes et al. 2012a, b) as:

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

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. $\mathbf{Q}$ is a matrix that denotes process parameters. The parameter $\mathbf{u}$ describes the trend of the population. $\mathbf{C}$ represents the coefficients of the covariates, and $\mathbf{c}_t$ represents the covariates through time t. $\mathbf{w}_t$ denotes the 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 populations are correlated to one another). We allowed $\mathbf{Q}$ to have different variances across sites (diagonals, $q^2_{i,i}$, were allowed to vary, while off-diagonals were set to zero), as process variation was assumed to differ across space (see Appendix S2 for model specifications).

The observation component, written in log space (Holmes et al. 2012a, b), is:

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

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 zeros and ones that assigns observations to a population structure. The number of sites (n) may be different from the number of populations (m) at time t (Ward et al. 2010). Observation errors, $\mathbf{v}_t$, were assumed to be uncorrelated and follow a multivariate normal distribution, with a mean of zero and a variance–covariance matrix $\mathbf{R}$. We set the diagonals in $\mathbf{R}$ ($r^2_{i,i}$) to have equal variance across sites for each species (but differing between species), as the same trapping methods were employed throughout the study, and to avoid over-parameterizing the models. Smaller-scale studies have found no difference in trappability for some species in this study (Greenville and Dickman 2009), but further work is required to test this assumption at larger spatial scales. The $\mathbf{R}$ off-diagonals were set to zero (see Appendix S2 for detailed information on model specification). Equations (1) and (2) comprise the MARSS model.

For each species, we tested four possible spatial population structures: asynchronous, oasis, productivity, and wildfire hypotheses, each modelled by assigning a matrix of ones and zeros via the $\mathbf{Z}$-matrix (see Appendices S1 and S2 for site selection and model formulation).

Covariates that might influence population dynamics were as follows. Annual rainfall from the prior year and spinifex cover were entered as covariates via the $\mathbf{c}$ matrix. The 1-year lag for rainfall was used to account for the time required for small reptiles to respond, via breeding, to a resource event. All variables were standardized by subtracting the mean and dividing by the standard deviation (z-scored) to allow direct comparisons between covariates to be made. De-meaning (i.e., via z-score transformation) the data allows the parameters $\mathbf{u}$ and $\mathbf{a}$ to be set to zero, which reduces computational problems when trying to estimate both $\mathbf{u}$ and $\mathbf{C}$ simultaneously (Holmes et al. 2012a). In addition, by de-meaning the dataset and setting $\mathbf{u} = 0$, we focused specifically on the effects of the covariates on the population estimates (see Appendix S2 for model formulation). Covariates (rainfall and spinifex cover) measured for each population (site) were modelled via the $\mathbf{c}$ matrix. Thus, four models were run for each species and the best-fitting model was chosen by the deviance information criterion (DIC) value.

We calculated 95 % credible intervals for each parameter and considered these significant if they did not cross zero. To allow for model convergence, each model was

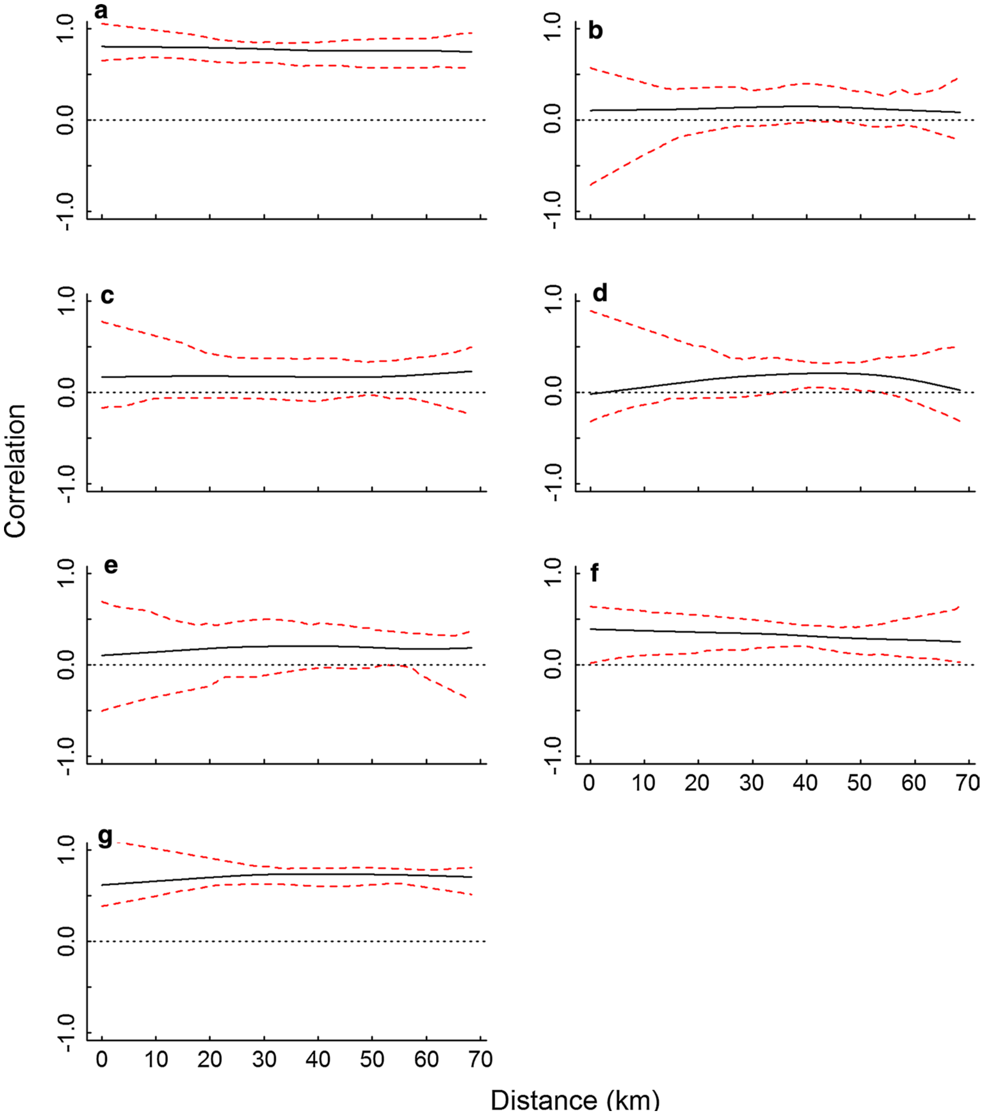

Fig. 2 Spatial cross-correlations (*solid line*) from 1998 to 2012 across nine sites in Central Australia of **a** annual rainfall, **b** *Ctenotus pantherinus*, **c** *Ctenotus ariadnae*, **d** *Ctenotus dux*, **e** *Lerista labialis,* **f** *Ctenophorus isolepis* and **g** *Ctenophorus nuchalis*. *Red dashed lines* represent 95 % confidence intervals (colour figure online)

fitted with three Markov chains, each having 300,000 Markov chain Monte Carlo (MCMC) iterations, thinning of 10 and the first 280,000 iterations discarded, leaving 6000 iterations saved (see Appendix S2 for description of priors, model formation and Appendix S3 for JAGS code). Inspection of diagnostic plots indicated that all models met statistical assumptions and models converged. Analyses were conducted in R 3.03 (R Core Team 2014) and JAGS 3.4.0 (Plummer 2013), using the R2jags 0.04–03 (Su and Yajima 2014) and rjags 3–13 (Plummer 2014) packages.

Results

The mean cross-correlation coefficient for annual rainfall across the nine study sites was 0.77 (CI 0.65 to 0.86) and did not change with distance between sites (Fig. 2a), suggesting regional synchrony in annual rainfall across our 8000 km^2 study region. In general, the timing of large rainfall events (>400 mm) was similar across the nine sites (Fig. S1). In total, 17,681 captures of individual reptiles were made over the period of study, including 12,570 of the six study species (Table S1), yielding an overall trap success rate of 8.6 % in relation to the total trapping effort.

Mean cross-correlation coefficients for the four species of skink were 0.13 (CI −0.02 to 0.33), 0.18 (CI 0.03 to 0.36), 0.16 (CI −0.05 to 0.39) and 0.19 (CI −0.002 to 0.41), for *C. pantherinus*, *C. ariadnae*, *C. dux* and *L. labialis*, respectively, indicating little synchrony across the nine populations and no evidence of change over distance between populations (Fig. 2b–e). Mean cross-correlation coefficients for the dragons, *C. isolepis* and *C. nuchalis,*

Table 1 The results of MARSS models for captures of reptiles (100 trap nights, log + 1 transformed), Simpson Desert, Central Australia

Model covariates	Rainfall	Spinifex cover	Process error (q^2)	Observation error (r^2)
Ctenotus pantherinus				
Population (burnt)	**0.35 (0.13 to 0.59)**	0.02 (−0.15 to 0.07)	0.29 (0.09 to 0.58)	0.85 (0.75 to 0.96)
Population (unburnt)	0.05 (−0.37 to 0.45)	−0.05 (−0.39 to 0.23)	0.47 (0.12 to 0.97)	
Ctenotus dux				
Population (burnt)	0.02 (−0.34 to 0.36)	0.07 (−0.24 to 0.37)	0.53 (0.25 to 0.92)	0.86 (0.76 to 0.97)
Population (unburnt)	−0.12 (−0.41 to 0.19)	−0.04 (−0.24 to 0.15)	0.22 (0.07 to 0.56)	
Ctenotus ariadnae				
Population (burnt)	0.01 (−0.25 to 0.27)	−0.04 (−0.23 to 0.20)	0.34 (0.10 to 0.76)	0.91 (0.79 to 1.04)
Population (unburnt)	−0.18 (−0.58 to 0.17)	−0.07 (−0.41 to 0.19)	0.37 (0.08 to 0.95)	
Lerista labialis				
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)	
Ctenophorus isolepis				
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)	
Ctenophorus nuchalis				
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)

Data were z-scored so that direct comparisons could be made. There was only one observation error (r^2) element for each species, as these were assumed to be equal for each sub-population. Each covariate was considered significant if the 95 % credible intervals (CI) did not cross zero and are in bold

were 0.31 (CI 0.16 to 0.46) and 0.72 (CI 0.64 to 0.81), respectively, indicating little evidence of synchrony for *C. isolepis*, but a high level of population synchrony for *C. nuchalis.* In addition, mean cross-correlation coefficients were not influenced by distance between the nine populations (Fig. 2f, g).

A one-state, synchronous MARSS population model showed that rainfall and spinifex cover did not influence *C. nuchalis* populations (Table 1). For species that did not show evidence of synchrony, the best predicting MARSS population models for the four species of skink, *C. pantherinus*, *C. ariadnae, C. dux* and *L. labialis*, was the wildfire model, suggesting that the populations of these species are structured into two sub-populations across the study region (Table 2, Fig. 3). The oasis model was the best predictor for *C. isolepis*, suggesting that this species is structured into two sub-populations (Table 2; Fig. 3). Annual rainfall from the prior year significantly influenced *C. pantherinus* populations in burnt regions, but rainfall and spinifex cover had little influence on the other species studied (Table 1). Process and observation errors were similar across all species examined, except for the observation error for *C. nuchalis,* which was lower than for all other species (Table 1).

Discussion

Our results provide little evidence that rainfall synchronizes reptile populations or directly influences population fluctuations in most of the study species, and suggest further that species are structured into populations in contrasting ways. As predicted from Moran's theorem, the mean spatial cross-correlation coefficient for *C. nuchalis*, the one species that exhibited evidence of synchrony, equalled the mean cross-correlation for annual rainfall, suggesting that rainfall may play a role in synchronizing populations of this species over the 8000 km^2 study region. However, further testing using MARSS models showed that annual rainfall did not significantly influence populations of this species (Table 1), thus suggesting that rainfall events do not directly drive population synchrony in this species and that an intermediary factor may be at play. Rainfall was only shown to be an important driver for *C. pantherinus* populations in burnt regions. There was little evidence of spatial population synchrony in the five other reptile species. The wildfire hypothesis was the best supported model for four species of skinks, *C. pantherinus*, *C. ariadnae, C. dux* and *L. labialis*, and the oasis hypothesis was the best supported

Table 2 Deviance information criterion (DIC) values for MARSS models describing four possible spatial sub-population structures, for five species of reptiles in the Simpson Desert, Central Australia

Model	DIC	ΔDIC	DIC weight
Ctenotus pantherinus			
Asynchronous	1213	606	0
Oasis	612	5	0.007
Productivity	718	111	0
Wildfire	**607**	0	0.99
Ctenotus dux			
Asynchronous	1245	638	0
Oasis	629	22	0
Productivity	722	115	0
Wildfire	**607**	0	1
Ctenotus ariadnae			
Asynchronous	1204	571	0
Oasis	640	7	0
Productivity	745	112	0
Wildfire	**633**	0	1
Lerista labialis			
Asynchronous	1237	603	0
Oasis	651	17	0
Productivity	747	113	0
Wildfire	**634**	0	1
Ctenophorus isolepis			
Asynchronous	1312	700	0
Oasis	**612**	0	1
Productivity	767	155	0
Wildfire	630	18	0

Data are based on 13–22 years of live trapping from nine sites. The smallest DIC, highlighted in bold, indicates the best-fitting model

model for *C. isolepis*, suggesting that these species are structured into two populations across the 8000 km^2 study region. Taking these results together, populations of our six study species are generally structured in space into one or two independent populations, of differing sizes, suggesting that landscape-scale population drivers are particularly important. However, there is little support for the Moran effect for all but one species in our highly variable desert environment.

Wildfire was important in structuring the spatial dynamics of *C. pantherinus*, *C. ariadnae, C. dux* and *L. labialis*, but these skinks showed no relationship with vegetation cover. These observations accord with past studies in showing that these species increase in abundance with age since fire (Letnic et al. 2004). However, contrary to our predictions, they suggest that vegetation cover, spinifex, may not drive the changes. Reptiles may respond to other habitat components or to invertebrates after wildfire. For example, wildfire may change termite abundance (Letnic et al. 2004) and remove vegetation, which in turn allows movement of sand. Loose sand allows easier movement for the termite specialist *L. labialis* and greater access to foraging areas (Greenville and Dickman 2005, 2009). Alternatively, predation risk may increase in the open areas created by wildfires (Daly et al. 2008). Predators can affect the demography of prey populations and access to resources (Downes 2001). In addition, grazing by native and introduced species may interact with wildfire, reducing vegetation recovery times or re-establishment of key habitat components (Driscoll et al. 2012). Thus, the removal of the dominant vegetation by wildfire may not have direct effects on reptile populations, but be mediated through complex biotic and abiotic interactions. Such habitat-mediated pathways of change are probably pervasive in disturbed ecological systems (Doherty et al. 2015), but remain relatively little studied.

Contrary to our expectations, life history traits were poor predictors of synchrony; species with a similar annual life cycle showed very different population patterns. Only one species with an annual life cycle, *C. nuchalis*, exhibited strong cross-correlations across the nine populations, while the best supported model for the other species, *C. isolepis*, was the oasis hypothesis. Oasis sites, such as ephemeral rivers and swamps, may provide refugia for *C. isolepis* during times of below-average rainfall. For example, oasis sites are more productive and have higher soil moisture levels than the surrounding desert (Free et al. 2013). They also harbour greater numbers of some prey groups, such as ants, which are a favoured prey source for *C. isolepis* (Daly et al. 2008; Free et al. 2013).

Rainfall is a limiting resource in desert environments and can drive strong bottom-up processes (Noy-Meir 1973). For some desert species, rainfall can drive regional synchrony, but species-level responses even then may be quite varied, even within the same family (Greenville et al. 2016). In addition, regional rainfall can be a good predictor of the abundance of species populations, but not perform strongly at local scales (Rodríguez and Ojeda 2015). Biotic interactions, such as top-down effects, may become important at the local scale, leading to complex interactions between biotic and abiotic factors at differing spatial scales (Ernest et al. 2000; Rodríguez and Ojeda 2015). Our findings suggest that for arid-zone populations of reptiles, spatial and temporal dynamics are structured by abiotic events,

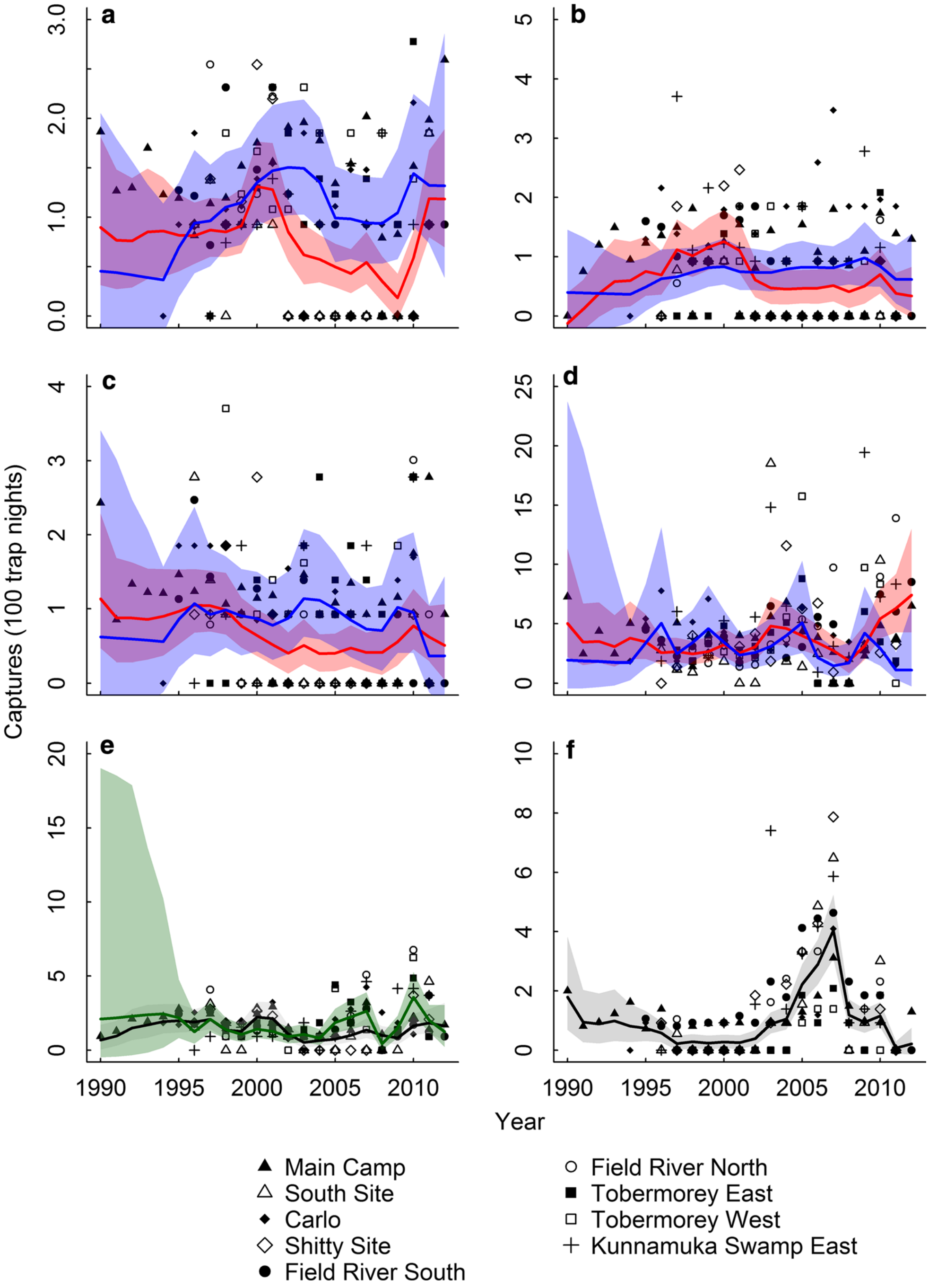

Fig. 3 Predicted population size (*line*) and captures (*dots*; captures/100 trap nights) from MARSS models for wildfire population model for **a** *Ctenotus pantherinus* (burnt: *red line*, unburnt: *blue line*), **b** *Ctenotus dux*, **c** *Ctenotus ariadnae*, **d** *Lerista labialis,* **e** oasis population model for *Ctenophorus isolepis* (oasis: *green line*, open desert: *black line*) and **f** 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 (colour figure online)

but individual responses to covariates at smaller spatial scales are complex and poorly understood.

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Author contribution statement The study was designed by AG, with input from GW, CD and VN. AG and VN performed the analyses, and AG wrote the first draft of the manuscript. AG, GW and CD collected the data. GW, CD and VN contributed substantially to all revisions of the manuscript.

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