Original article

Booming during a bust: Asynchronous population responses of arid zone lizards to climatic variables

John L. Read [a,*], Kelli-Jo Kovac [b], Barry W. Brook [a], Damien A. Fordham [a]

[a] Environment Institute, School of Earth and Environmental Sciences, University of Adelaide, Australia
[b] Environment Section, BHP Billiton Olympic Dam, PO Box 150, Roxby Downs, SA 5725, Australia

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ABSTRACT

The productivity of arid environments and the reproductive success of vertebrates in these systems, are typically thought to be primarily influenced by rainfall patterns. Data from our 15 year study at an Australian arid zone site reveals asynchronous demographic responses to rainfall and other climatic variables among different lizard species. We show that, in addition to precipitation, key demographic rates (fecundity, recruitment and survival) are correlated strongly with temporal variability in temperature, during and prior to the breeding season, and also to the density of sympatric lizard species. There were nine-fold fluctuations through time in the relative abundance of two similar-sized *Ctenotus* species, and asynchronous recruitment success and survival among other species, despite the absence of direct anthropogenic affects Understanding the drivers and magnitude of the substantial natural variability in arid-zone lizard assemblages is integral to predicting and interpreting their responses to future land use or climate-change scenarios.

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1. Introduction

Rainfall is a key driver of arid ecosystems (Morton et al., 2011). The reproductive output of some arid zone lizard species responds dramatically and predictably to increased food resources (Ballinger, 1977; Dunham, 1981; Pianka and Vitt, 2003), or changes in vegetation cover (Heatwole, 1970; Read and Cunningham, 2010), following above-average precipitation. Furthermore, rainfall can directly affect intergenerational demographics (Marquis et al., 2008); and increased recruitment can occur following consecutive favourable rain-induced growing seasons, allowing some lizard species to emigrate to marginal habitats (Whitford and Creusere, 1977).

However, field studies on other arid zone lizards suggest life-history and reproduction constraints unrelated to food availability or vegetation structure (Perry and Dmi'el, 1994; Niejalke, 2006). Temperature is an important timing cue for lizard reproduction (Licht, 1972) and can affect adult survivorship, body size and fecundity (Chamaille-Jammes et al., 2005). Since temperature is an integral determinant of resource utilisation (Dunham, 1981), changes in temperature affect vital life-history traits (Adolph and Porter, 1993; Smith et al., 1995). Mean temperature of incubation

and variance about the mean, affect lizard hatchling phenotypes (Packard and Packard, 1988) and hatching success is dramatically reduced at incubation temperatures slightly cooler (Shine and Elphick, 2001) or hotter (van Damme et al., 1992) than optimal. Shorter incubation durations at warmer temperatures result in earlier hatching dates, which can enhance lizard survivorship by provisioning hatchlings with greater food reserves and foraging time before the onset of winter (van Damme et al., 1992; Qualls and Shine, 2000; Pianka and Vitt, 2003). Furthermore, lizards incubated at their optimum temperatures, even for brief periods, exhibit higher mass, increased locomotor performance, improved anti-predator tactics and lower mortality rates than lizards incubated at cooler or hotter temperatures (van Damme et al., 1992; Shine and Elphick, 2001). Changes in cloud cover, irrespective of temperature, can also affect lizard recruitment and growth rates (Niejalke, 2006; Hare and Cree, 2010).

Many ecological impacts of recent climate change are already evident worldwide, at both the species and community levels (Rosenzwieg et al., 2008), with these effects likely to be amplified with predicted future climate change (Thomas et al., 2004). Due to their limited dispersal capabilities and the profound influence of slight temperature changes on reptile activity (Bennett and John-Alder, 1986), gender (Wapstra et al., 2008) and vital rates (see above), lizards are potentially more vulnerable to climate change than broad-ranging endothermic bird and mammal species

(Henle et al., 2008; Sinervo et al., 2010; Huey et al., 2010). Long-term, meticulously-controlled field studies are typically necessary to detect drivers of recruitment success and resource dynamics in arid zone fauna assemblages (Tinkle and Dunham, 1986; Smith et al., 1995; Langlands et al., 2006). However, with the exception of a study comparing the influence of rain on the population dynamics of two agamids (Dickman et al., 1999), such studies facilitating systematic investigation of the relative influence of climatic and environmental variables on structuring Australian arid zone lizard assemblages are lacking.

Here we use capture-mark-recapture modelling of a consistent 15 year dataset to quantitatively investigate the influence of environmental and climatic parameters on recruitment, survival and abundance of the six most abundant lizards at an Australian arid zone locality. Three of these species were *Ctenotus* skinks, which have undergone a considerable evolutionary radiation in arid Australia and are typically the most abundant and diverse genera of diurnal lizards at many sites (James, 1991a; Pianka and Vitt, 2003). The other three species were diplodactyline geckoes, which are typically the most abundant nocturnal reptiles throughout many habitats in arid Australia (Pianka, 1986; Read and Owens, 1999). The 'PITGRID' research site at Roxby Downs has the rare advantage of being a long-term, high capture site without inter-annual variability in fire, stock numbers or sampling methodology. Furthermore, because each sampling session is conducted over a one month period, the considerable effects on reptile capture rate of daily fluctuations in temperature, rain and moon phase (Read and Moseby, 2001), are largely negated.

The principal aim of this study is to test the *a priori* hypothesis that productivity driven by rainfall is the key driver of annual variability in Australian arid-zone reptile assemblages. In addition, by modelling the main determinants of variability in key demographic parameters across a range of abundant lizard species, we are able to make generalisations regarding how predicted climate change is likely to affect the composition and abundance of Australian arid zone lizard assemblages.

2. Methods

2.1. Study site

The PITGRID research site (30 29′S, 136 55′E) occupies 1 ha of chenopod shrubland, 18 km north of Roxby Downs in northern South Australia. Although variability in grass and surface stone cover and soil type (from heavy clay to sand) delineate five discernable sub-habitats, *Atriplex vesicaria* and *Maireana astrotricha* dominate the perennial vegetation throughout the 100 m by 100 m unbounded capture-mark-recapture study site (Read, 1995a). Summer maxima frequently exceed 40 °C and winter minima occasionally decline below 0 °C, with sporadic summer or winter rains failing to reach the average annual rainfall of 166 mm in 60% of years (Read, 1995b). The study site was particularly valuable for assessing the influence of climatic variables on lizard assemblages because two of the dominant ecological processes in arid ecosystems, fire and livestock grazing, were controlled throughout this 15 year study. No livestock had access to the site since low cattle numbers with minimal impact on reptile communities were removed in the mid 1980's (Read, 1992; Read and Cunningham, 2010) and there was no evidence of historical or contemporary fires in the fire-retardant chenopod shrubland.

2.2. Study species

Although 34 reptile species have been recorded from the study site, six species represented the majority of captures, and these were selected to run the exploratory analysis without risk of overfitting capture-mark-recapture models. The most abundant *Ctenotus* at the study site were the medium-sized species *Ctenotus regius* (number marked individuals [n] = 452) and *Ctenotus leonhardii* (n = 313) and the small *Ctenotus schomburgkii* (n = 716). Each of these species are relatively sedentary and unspecialised insectivores, with *C. leonhardii* frequently exceeding five years of age and *C. regius* and *C. schomburgkii* reaching three and four years respectively (Read, 1998). *Diplodactylus conspicillatus* (n = 384), and *Rhynchoedura ornata* (n = 843) are termite specialists and consistently produce multiple clutches of two eggs each summer, whilst *Lucasium stenodactylum* (n = 361), is a dietary generalist with more variable reproductive output (Pianka, 1986). Both *D. conspicillatus* and *L. stenodactylum* have been recorded breeding for three successive years, whereas the shorter-lived *R. ornata* seldom breeds in more than one year (Read, 1999).

2.3. Capture-mark-recapture methods

The PITGRID array consisted of 401 cylindrical pits, 500 mm deep and 150 mm in diameter, dug flush with the ground level on a 5 m grid that excluded every second perimeter pit. Pits were sealed with snug sewer-pipe caps when not in use. Each 4–5 week trapping session comprised ten days when all pits were opened, with each of the ten trapping days separated by at least one 24 h period when all pits were closed to allow free movement of individuals on the study site. The PITGRID array was trapped in both November and February each year between 1991 and 2006. Traps were checked and closed at dawn, with all captures transported to an air-conditioned laboratory for detailed study. Each individual was permanently marked with a unique toe-clip combination by removing the terminal section of up to four digits. The size, sex and reproductive condition of recaptured individuals were compared with previous captures to account for rare identification problems arising from injuries or erroneous readings of toe-clips. All suspect individuals were removed from the analysis. Snout-vent length was measured to the nearest millimetre and weight was recorded on an electric balance to the nearest 0.1 g. Skinks were sexed by attempting to evert hemipenes, and gekkonids by the more enlarged bulbous postanal region of adult males. Gravid geckoes were detected through eggs clearly visible through the belly wall and female skinks were palpated to determine presence of eggs. Animals smaller than the third percentile of gravid females were classed as immature (Table S1, see Read, 1998, 1999). All animals were held in the air-conditioned laboratory until evening, when they were returned to their exact location of capture, with the traps then closed.

2.4. Environmental variables

Activity indices of the dominant large herbivores (kangaroos and rabbits) and feral predators (cats and foxes) were estimated each January by spotlight counts along a fixed 20 km transect adjacent to the study site (Bowen and Read, 1998). Vegetation condition was assessed through a series of four colour photopoints taken at the beginning of each annual sampling session. A condition score, ranging from 0 to 7 (sum of three categorical descriptors), accounted for cover and seed production of chenopod shrubs (*Maireana* and *Atriplex* spp.) and ephemeral species (principally grasses) and incorporated a greenness index (Table S2).

Long-term daily rainfall and temperature data for the Woomera (Station number = 16001), Roxby Downs (16040) and Andamooka (16065) weather stations (those in closest proximity to the PITGRID) were obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au) and used to calculate: (a) cumulative

seasonal rainfall averages for the study region; and (b) the average of the 20 most extreme daily minimum and maximum temperatures in each season (*spring, winter, autumn* and *summer*). Temperature extremes were considered more important than averages since warm days in cool weather and mild temperatures in very hot summers are more influential over lizard activity than average temperatures. Temperature extremes are also more likely to create lethal or unfavourable conditions for lizard activity and egg development. Lizard reproductive output and survival may be influenced by resource availability before, during or immediately following the breeding season, temperature regimes and soil moisture during the incubation period. Thus, several different rainfall and temperature parameters were investigated in our demographic models. Rainfall variables used in the analysis were cumulative rainfall between: (i) 0–3 months prior to trapping (*spring*); (ii) 4–6 months (*winter*); (iii) 7–9 months (*autumn*); (iv) 10–12 months (*summer*); (v) 13–15 months (*prev. spring*); (vi) 0–6 months (*winter* & *spring*); (vii) 7–12 (*autumn* & *summer*); and (viii) 0–12 months (*annual*). To avoid multi-colinearity, rainfall variables were modelled separately; as were extreme temperature averages.

The Southern Oscillation Index (SOI), a measure of fluctuations in the air pressure difference between Tahiti and Darwin, Australia, is a useful predictor of rainfall in Australia (Ropelewski and Halpert, 1989) and possibly abundance of arid zone vertebrates at local scales (Letnic et al., 2005; Letnic and Dickman, 2006). Strongly positive values of SOI (>5.5; La Niña) are associated with periods of high rainfall and strongly negative values (<5.5; El Niño) are associated with low rainfall, particularly during winter and spring across eastern and northern Australia (Chiew et al., 1998). SOI cumulative averages were calculated using BOM National Climate Centre data (ftp://ftp.bom.gov.au/anon/home/ncc/www/sco/soi/soiplaintext.html; accessed 17/4/2008): 0–6 months (June–November), 2–8 months (April–September) and 12–16 (previous June–November) months prior to trapping.

The Indian Ocean Dipole (IOD) is a coupled ocean and atmosphere phenomenon in the equatorial Indian Ocean that affects the climate of Australia and other countries that surround the Indian Ocean basin (Saji et al., 1999). IOD has been positively correlated with surface air temperatures in subtropical Australia during spring (Saji et al., 2005), and negatively correlated with winter rainfall in central Australia (Ashok et al., 2003) and extreme rainfall events in southwest Western Australia (England et al., 2006). IOD cumulative monthly averages were calculated based on the NOAA OI SST data (http://www.jamstec.go.jp/frcgc/research/d1/iod/: accessed 4/06/2008), which uses a combination of ship, buoy and satellite data (Reynolds et al., 2002).

2.5. Population modelling

2.5.1. Survival and recapture models

Animals caught in either November or the following February were pooled and these trapping occasions were treated as a single interval for estimation of survival (ϕ) and recapture probabilities (p). The reason for pooling data were twofold: it allowed us to easily distinguish between yearly cohorts of juveniles; and goodness of fit tests (White et al., 2001; see below) generally demonstrate a more adequate fit between simpler models (with annual, rather than bi-annual, time steps) and the data, across species.

Program Mark 5.0 (White and Burnham, 1999) was used to estimate ϕ and p of lizards between years (1991/92–2005/06). Identical candidate model sets were formulated *a priori* and implemented in Program Mark for each species. We used the multi-model inference approach advocated by Burnham and Anderson (2002) to interpret statistical models; Akaike's Information Criterion corrected for small sample sizes (AIC$_c$) was used to

rank the models by strength of evidence, and calculate the relative weights of evidence for each (w_i). We used the two stage modelling approach, advocated by Lebreton et al. (1992), for capture-mark-recapture data whereby recaptures are initially modelled and survival is controlled. How to best fix survival remains unresolved. Some authors set survival as high and variable (e.g., Lebreton et al., 1992), others use the most saturated model (e.g., Pardon et al., 2003) or the null model (e.g., Firth et al., 2010). We choose the later approach, which first maximises model strength in explaining recapture variability (which can influence survival estimates; Conroy and Carroll, 2009), and then survival variability. After the optimal recapture model was selected, a parsimonious survival model was sought. Climatic and environmental variables that may influence the survival and recapture rates of reptiles were treated as across-population covariates. Juvenile and adult animals were segregated according to size (see above) and modelled as a two level factor (*group*). The influence of inter-specific interactions was also investigated by using the abundance of other lizard species from the previous year as covariates (see below).

Initially, we constructed a candidate model set (Table S3) to investigate whether climate and environmental variables (and their interaction) influence survival and recapture probabilities and whether age-class is an important factor. We hypothesised *a priori*, based on past field experience and a review of the relevant herpetological literature (see Introduction), that survival and recapture rates of skinks and geckos would be influenced by the following factors: (i) the timing and quantity of rainfall, impacting resource availability; (ii) extreme seasonal temperatures, influencing embryonic development and foraging activity; (iii) a strongly positive SOI, increasing resource availability (Letnic and Dickman, 2006); (iv) positive IOD, negatively influencing rainfall (Ashok et al., 2003; England et al., 2006) and, in turn, resource availability; (v) the abundance (assumed to indicate predatory activity) of cat and foxes (Read and Bowen, 2001); (vi) rabbit and kangaroo numbers, both directly (through grazing, causing reduced food and habitat); and, in the case of rabbits, indirectly (promoting predator abundance; Read and Bowen, 2001); (vii) vegetation condition – a surrogate for food availability and habitat quality; and (viii) size class, owing to size-related biases in predator detection and inter-specific interactions. We used AIC to select the best model in terms of parsimony (Burnham and Anderson, 2002). An analysis of deviance was used to assess the relative effects of covariates on survival and recapture rates (R^2), defined as [DEV (constant model) – DEV(covariate model)/(DEV(constant model) – DEV(time-dependent model)] (Le Bohec et al., 2008).

Survival and recapture probabilities were model averaged using Akaike Weights (w_i), so as to include model selection uncertainty in the estimates of parameter precision (Buckland et al., 1997). Goodness-of-fit of the model to the data was tested for each species using a parametric bootstrap approach. The over-dispersion quasi-likelihood parameter indicated adequate fit of the model to the data for all species except *R. ornata*. Model output for *R. ornata* was adjusted using a variance inflation factor (*c-hat* = 1.28) following White et al. (2001).

To investigate the role of inter- and intra-specific interactions on survival probabilities, we constructed a second candidate model set using species' abundances as a proxy for potential inter-specific interactions (Table S4). Recapture probabilities were used to estimate population density for each species (See Estimating density), which was subsequently modelled as an across-population covariate. Survival models with $w_i > 0.1$ (from survival analysis stage 1, where sum of w_i for all models = 1) were re-run using a reduced capture-mark-recapture (CMR) time series (1992/93-2005/06) and compared to models parameterised to represent inter- and intra-specific interactions. Species' abundance

in the previous year was used as a surrogate to model intra-specific interactions. Inter-specific interaction was modelled as an immediate and a delayed response. Likely ecological interactions were identified *a priori* according primarily to dietary overlap: (i) *R. ornata*, *D. conspicillatus* and to a lesser extent *C. schomburgkii* are termite specialists; and (ii) *C. regius* and *L. stenodactylum* are generalist insectivores. We also explored the possibility that skink abundance could influence survival rates through a predator/prey interaction; *C. leonhardii* occasionally preys upon *C. schomburgkii* (Read, 1998).

2.5.2. Estimating density and population growth rate synchrony

Recapture probabilities were used to estimate density per ha using the Horvitz−Thompson type estimator, accounting for capture area [$N_i = (n_i/p_i)/a_i$: Seber (1982)], where n_i is the number of animals captured, p_i is the estimated recapture probability obtained from the Cormack−Jolly−Seber survival modelling, a_i is the area of the trapping grid and N_i is estimated population abundance in the *i*th year. Approximate 95% confidence intervals were derived from the model-averaged standard error (SE) of p_i based on a normal approximation, whereby $p_i \pm (1.96*SE)$ was substituted in the Horvitz−Thompson equation given above (Fordham et al., 2007).

Pearson moment cross correlation coefficients were calculated by using first-differenced time series of log abundance (n/ha) to test for synchrony of population growth rates for different lizard species (see Bjornstad et al., 2009). Significant levels were obtained through 1000 randomized iterations and we elected to use $\alpha < 0.01$ to indicate synchrony.

2.5.3. Juvenile recruitment models

Gaussian-distributed general linear mixed-effects models (GLMM), with identity link functions were used to investigate environmental drivers of recruitment amongst skinks and geckos. Species was modelled as a random effect. Temperature, rainfall, resource availability and adult abundance, variables presumed to influence juvenile recruitment amongst central Australian reptiles, were modelled as fixed effects. Specifically, we modelled: (i) cumulative rainfall over the six months prior to trapping; (ii) vegetation condition; (iii) average of the 20 coolest night-time temperatures for each season; (iv) average of the 20 hottest temperatures for spring and summer (v) average SOI and IOD, 12−18 months, expressed in modelling shorthand as (SOI[prev. June−Nov]) and 2−8 months (IOD[April−Sep.]) prior to trapping, respectively; and (vi) adult abundance in the previous year (abund). Multi-term models were also considered (IOD*rain[winter & spring]; rain[winter & spring]*veg.). Abundance data (with the exception of *L. stenodactylum*) were normalized using a log transformation (Crawley, 2007).

Initial interrogation of our data suggested that juvenile density in a given year can vary greatly between closely-related sympatric lizards. Therefore we used variance components analysis to assess the importance of the random effect *species* (Crawley, 2007). Owing to the strength of the random effect, we concluded that generalized mixed effects models for skinks and geckos should not be simplified to generalized leased squares models (Pinhero and Bates, 2000). All generalized linear mixed effects models were fitted using the lmer function of the lme4 package in the R statistical package (R Development Core Team, 2005).

Species' density in the previous year and competitor abundances during the immediate trapping session were used to investigate the influence of intra- and inter-specific interactions using Gaussian type general linear models (GLM) with identity functions. Using vegetation condition as a surrogate for resource availability, we investigated the possibility that inter-specific

interactions may be more pronounced in poor years. The candidate model set also included an index of cumulative competitor abundance in the previous year and environmental parameters identified (using GLMM; $w_i > 0.1$) as having a general influence on skink and gecko recruitment.

2.5.4. Fecundity models

Binomial GLMs with logit-link functions were used to estimate the statistical relationship between the proportion of gravid/non-gravid geckos and potentially important environmental variables: (i) average of the 20 coolest night-time temperatures for spring, summer and winter; (ii) cumulative winter and spring rainfall; and (iii) vegetation condition. A multi-term model was also tested (rain [winter & spring]*veg.). We restricted our analysis to geckos, primarily because egg detection is less reliable in skinks, owing to eggs being less visible and problems regarding the accuracy of palpation.

The goodness-of-fit to the data for all GLMs and GLMMs were tested following methods outlined by Crawley (2007). Weighted model averaged coefficients and standard errors were calculated using all models with $w_i > 0.10$, after re-scaling so that the total weights for those models that contained any given fixed effect summed to 1.

3. Results

R. ornata and *C. regius* populations reached modelled densities of over 300 per hectare and even the least abundant study species, *L. stenodactylum*, reached modelled densities of 85 per hectare during the study period (Fig. 1). These estimates are likely to slightly overestimate densities as the sampling area exceeds the unbounded 1 ha trapping grid.

3.1. Density change synchrony

We found support for synchrony in the annual density variation between only two pairs of species, *D. conspicillatus* and *L. stenodactylum* ($p = 0.008$) (Table 1). By contrast, there was no support for synchrony between any of the gecko densities with any skink densities ($p > 0.1$, Table 1), indeed peaks and troughs in densities seldom coincided throughout the study period (Fig. 1). Furthermore, not only was the ratio of the similar-sized *C. leonhardii* to *C. regius* modelled densities not synchronous (Table 1) but the ratio of these species to each other reversed from 0.2:1 in 1994 to 1.9:1 in 2004.

3.2. Variability in environmental predictors

Vegetation condition responded to heavy rainfall events in 1989, 1992, 1993, 1997 and 2001 and declined during a period of below average rain from 2002 to 2006 to its poorest conditions of the sampling period (Fig. 2). Rabbit, cat and fox numbers were high from 1992 to 1996, dropped abruptly following the spread of the rabbit calicivirus through the region (Read and Bowen, 2001) and stayed low until 2000. Rabbit and cat numbers rose gradually from 2001, but did not reach pre-1996 levels, whilst kangaroo numbers tended to increase slowly throughout the monitoring period (Fig. 2).

The mean of each years 20 coolest winter daily temperatures varied from 2.7 °C to 4.5 °C, whilst the annual mean of the 20 coolest summer temperatures ranged from 13.4 °C to 17.7 °C (Fig. S1). Warmest mean annual summer maxima ranged from 38.7 °C to 43.9 °C, whilst warmest winter temperatures ranged from 21.0 °C to 25.0 °C (Fig. S1). Although annual temperature trends were not consistent across all seasons, 2004−2006 tended
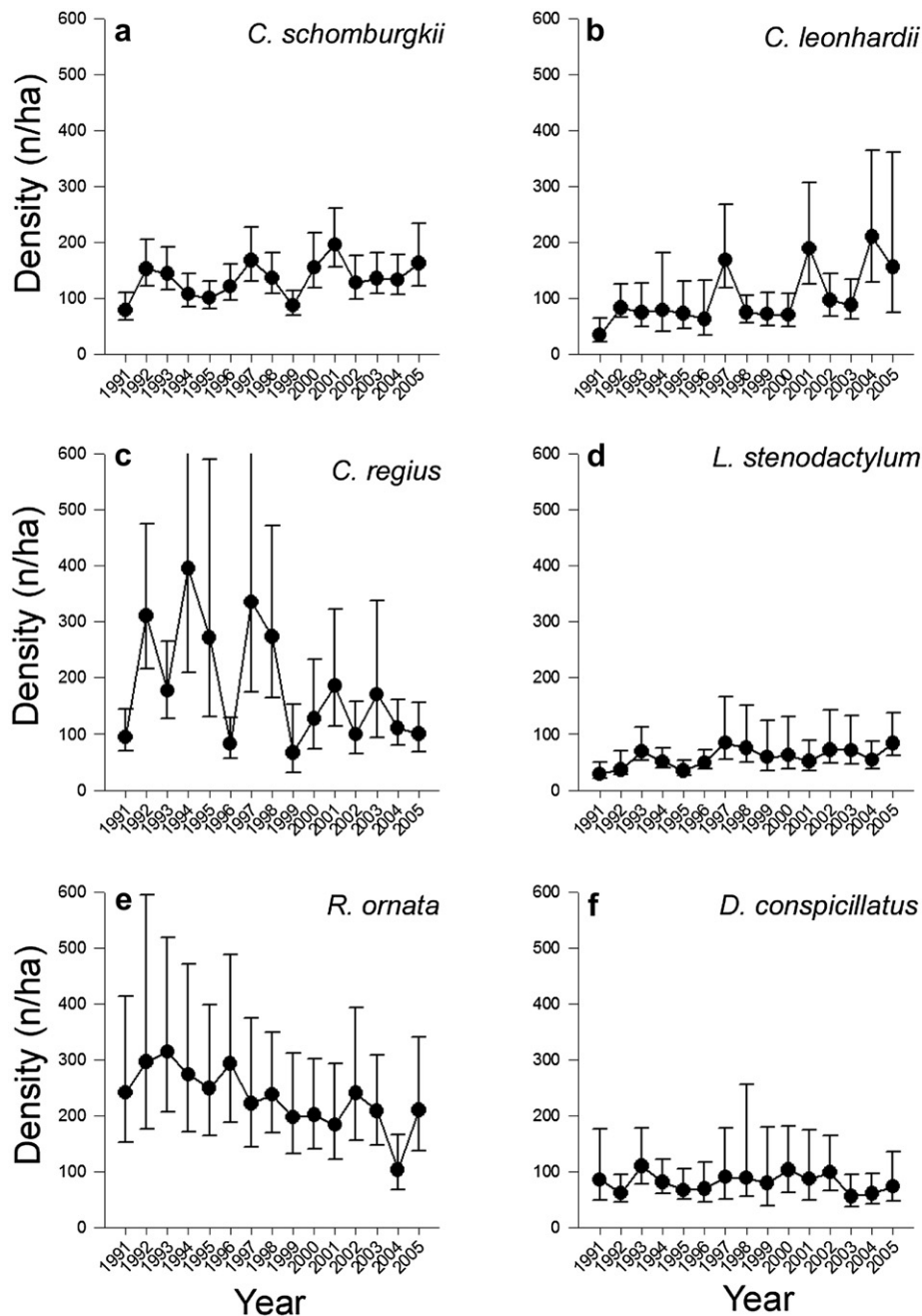
Fig. 1. Horvitz–Thompson type annual density estimate (*n*/ha) between 1991 and 2005 for three species of skink, *Ctenotus schomburgkii* (a) *Ctenotus leonhardii* (b) and *Ctenotus regius* (c); and three species of gecko, *Lucasium stenodactylum* (d), *Rhynchoedura ornata* (e) and *Diplodactylus conspicillatus*. Bars represent 95% confidence intervals.

to have the hottest days, with 1992 and 1997 both experiencing the coolest and wettest days (Fig. 2 & Fig. S1).

3.3. Recapture probabilities

Skink recapture probabilities (*p*) varied between species, two of the three species exhibited high year-to-year variation (Fig. S2). The most parsimonious *p* model for *C. leonhardii* included a positive interaction between fox density and rabbit density, negatively impacting upon recapture success (Table S4). There was essentially equal support for the top six ranked *L. stenodactylum* recapture models (Table S4). Cumulative rainfall during summer and autumn had the largest influence on *p* for *R. ornata*. For *D. conspicillatus*, recapture probabilities varied in response to average monthly SOI

during the previous June–November period (12–18 months prior to trapping; Table S4).

3.4. Survival estimates

Modelled averaged annual survival estimates (ϕ) for *C. schomburgkii* ($\phi = 0.4-0.6$) and *C. regius* ($\phi = 0.5-0.7$) displayed less variation than *C. leonhardii*, which exhibited annual ϕ from 0.35 to 0.95 (Fig. 3). Gecko survival probabilities tended to be lower ($\phi = 0.3-0.5$) than those for skinks and showed less year-to-year variability (Fig. 3).

Skink survival probabilities were correlated with rainfall, inter-specific interactions and temperature (Table 2). The negative interaction between average IOD (April–September) and

Table 1
Cross-correlation coefficients for inter-specific comparisons of population growth rates (first-differenced time series of log-abundance) among 6 lizard species at the PITGRID site. Cross-correlations marked by two asterisks (**) are significant at the $\alpha = 0.01$ level, none are significant at $\alpha = 0.001$ level. Significant levels were obtained through randomization (number iterations = 1000).

	C. leonhardii	C. regius	L. stenodactylum	R. ornata	D. conspicillatus
C. schomburgkii	0.496	0.564	0.299	0.143	0.04
C. leonhardii		0.474	−0.059	−0.473	−0.102
C. regius			0.086	−0.062	−0.215
L. stenodactylum				0.479*	0.565**
R. ornata					0.141

Significance of * is $\alpha = 0.05$.

cumulative rainfall during winter and spring had the largest (negative) influence on survival of *C. leonhardii*, with little support for all other models. The survival of *C. schomburgkii* was correlated with autumn rainfall and extreme minimum temperature events in autumn. There was essentially equal support for both of these single-term models, but less support for all other models (Table 2). Climatic variables had a less pronounced effect on *C. regius*; inter-specific interactions had the largest influence, with some support for the influence of rainfall in the previous spring (Table 2).

Survival in *R. ornata* was not adequately explained by any of the covariate models, with the null (which assumes temporally invariant survival) being among the top ranked models (Table 2). The most parsimonious model for *L. stenodactylum* included the

individual group factor age-class: survival being lower for juveniles than adults (Fig. 3). However, there was also support for: (i) a response to *L. stenodactylum* abundance in the previous year; and (ii) a multi-term model with *C. regius* abundance (as a competitor) and vegetation condition (Table 2). There was some evidence to suggest that *D. conspicillatus* survival is influenced by year-to-year variation in extreme temperature events in spring (*spring max.*) and autumn rainfall (*autumn*).

3.5. Juvenile recruitment

Annual juvenile recruitment fluctuated by over an order of magnitude for *C. leonhardii* and *C. regius* but was more stable in
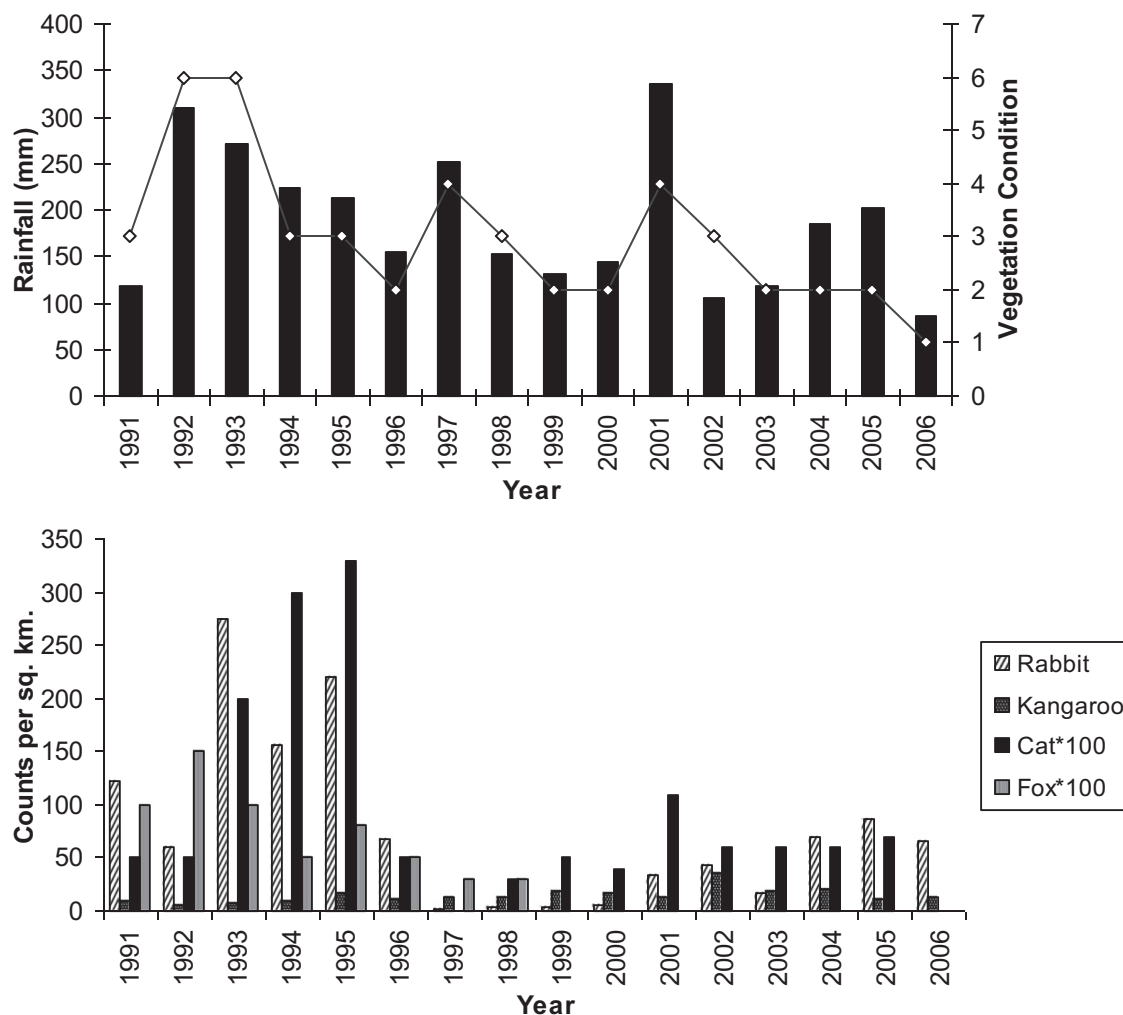

Fig. 2. a) Rainfall (mm, shown as solid columns) and vegetation condition at the PITGRID site from 1991 to 2006. b) Transect counts (per sq km) of key herbivores and exotic predators at the PITGRID site from 1991 to 2006.
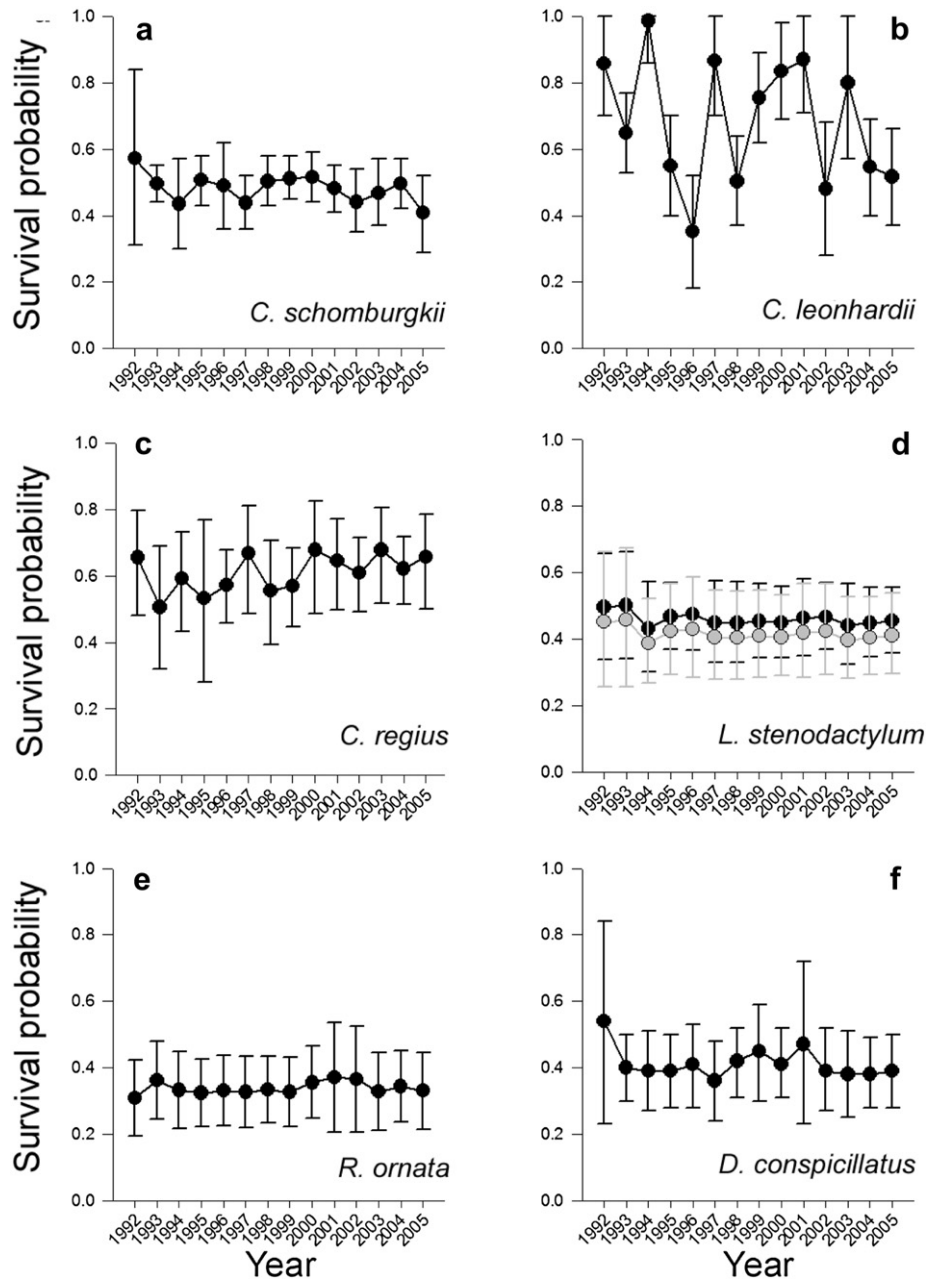
Fig. 3. Model averaged annual survival probabilities between 1991 and 2005 for three species of skink, *Ctenotus schomburgkii* (a) *Ctenotus leonhardii* (b) and *Ctenotus regius* (c); and three species of gecko, *Lucasium stenodactylum* (d), *Rhynchoedura ornata* (e) and *Diplodactylus conspicillatus* (f). Note that for *Lucasium stenodactylum*, juvenile (grey scale) and adult (black) survival rates differed.

C. schomburgkii (Fig. S3). Vegetation condition exerted the largest influence on juvenile skink abundance, explaining 18% of the deviance compared to the null model (Table S5), indicating that abundance across species is regulated by factors in addition to vegetation. Vegetation condition positively influenced juvenile *C. regius* abundance, explaining 41% of the deviance, when compared to the null model (Tables 3 and 4). There was also good support for modelling *C. regius* juvenile recruitment as a function of *L. stenodactylum* abundance in the previous year as well as vegetation condition. The most parsimonious model for *C. schomburgkii* juvenile recruitment included vegetation condition and *C. leonhardii* abundance (Dev = 80%; Table 3), both being positively correlated with *C. schomburgkii* abundance (Table 4). There was good support for the null as well as the

most parsimonious model ($\Delta AIC_c < 2$) for *C. leonhardii* recruitment.

Density estimates for juvenile geckos differed between species, tending to be lower (especially in the early years) and less variable for *L. stenodactylum* and *D. conspicillatus*, compared to *R. ornata* (Fig. S3). Juvenile recruitment (across species) for geckos was not influenced by vegetation condition. There was some evidence to suggest that IOD (April–September) and extreme maximum daily temperature events in autumn (autumn max) may influence gecko recruitment, but both terms explained relatively little overall variance (6 and 4% respectively; Table S5). There was no support for *D. conspicillatus* and *R. ornata* juvenile recruitment being influenced by inter-specific or intra-specific interactions or any other modelled parameters (Table 3). In both cases there was good support for the

Table 2
Cormack–Jolly–Seber mark-recapture summary survival model set showing: Akaike's information criterion (AIC_c), number of parameters (k), deviance (Dev), change in AIC_c compared to the best-ranked model (ΔAIC_c) and model weights (w_i) for three skinks (*Ctenotus schomburgkii*, *Ctenotus leonhardii* and *Ctenotus regius*) and three species of gecko (*Diplodactylus conspicillatus*, *Lucasium stenodactylum* and *Rhynchoedura ornata*). Survival (Φ) and recaptures (p) were modelled as a two-step process (see Methods). Model output for *R. ornata* was adjusted using a variance inflation factor, providing $QAIC_c$ and $\Delta QAIC_c$ values.

Species	Model	AIC_c	k	Dev	ΔAIC_c	w_i	R^2
C. schomburgkii	$\phi(rain[autumn])$	1270.55	4	1262.50	0.00	0.40	0.72
	$\phi(temp.[autumn\ min.])$	1271.26	4	1263.21	0.70	0.29	0.70
C. leonhardii	$\phi(DMI[April–Sep]*rain[winter\ \&\ spring])$	846.12	8	829.77	0.00	0.95	0.75
C. regius	$\phi(C.\ regius[previous\ year])$	732.93	6	720.76	0.00	0.43	0.20
	$\phi(rain[previous\ spring])$	734.69	6	722.52	1.76	0.18	0.12
	$\phi(cat^+rabbit[count\ high])$	735.29	7	721.06	2.36	0.13	0.19
	$\phi(L.\ stenodactylum\ adult\ abundance)$	735.47	6	723.30	2.54	0.12	0.09
L. stenodactylum	$\phi(group)$	578.58	6	566.36	0.00	0.27	0.21
	$\phi(L.\ stenodactylum[previous\ year])$	580.12	6	567.90	1.54	0.12	0.13
	$\phi(C.\ regius^+vegetation)$	580.52	7	566.23	1.77	0.11	0.22
R. ornata	$\phi(D.\ conspicillatus\ adult)$	589.77[a]	5	744.61	0.00[b]	0.18	0.22
	$\phi(.)$	590.07[a]	4	747.57	0.30[b]	0.16	0.00
	$\phi(D.\ conspicillatus)$	590.63[a]	6	745.71	0.88[b]	0.12	0.14
D. conspicillatus	$\phi(temp.[spring\ max.])$	475.63	4	467.53	0.00	0.28	0.34
	$\phi(rain[autumn])$	476.26	4	468.15	0.63	0.20	0.29
	$\phi(.)$	477.62	3	471.56	2.00	0.11	0.00
	$\phi(group)$	477.70	4	469.57	2.07	0.10	0.17

Environmental variables include seasonal rainfall (e.g., *rain*[*autumn*]), rainfall across 6 months (e.g., *rain*[*winter & spring*], *rain*[*summer & autumn*]) and lagged rainfall (e.g., *rain* [*previous spring*]); minimum and maximum seasonal temperature (e.g., *temp*[*autumn min.*]; *temp*[*spring max*]); and a measure of the strength of the Southern Oscillation Index (SOI) and Indian Ocean Dipole (IOD) between June–November and April–September, respectively. The relationship between rabbits and fox and cat density was modelled as interactive (e.g., *fox*rabbit*, *cat*rabbit*) and additive (e.g., *cat*+*rabbit*[*count high*]). Intra and inter-specific species interaction parameters were tested using total relative abundance (e.g., *D. conspicillatus*) and adult relative abundance (e.g., *D. conspicillatus adult abundance*); lagged abundance was also modelled (e.g., *C. regius*[*previous year*]). Size was modelled as a grouped factor (*group*) and the time constant model (.) was considered (see Methods). Note that only models with $w_i > 0.1$ are shown.
[a] $QAIC_c$.
[b] $Q\Delta AIC_c$.

null model ($\Delta AIC_c < 2$). *L. stenodactylum* juvenile density was positively correlated with *C. regius* abundance in the previous year (Tables 3 and 4), however the explained deviance was modest (Dev = 30%), suggesting that additional factors influence *L. stenodactylum* juvenile recruitment. Including vegetation index as an additive factor within the model had support (Dev = 38%).

More generally, we surprisingly found little to no support for adult abundance in the previous year being a predictor of juvenile abundance (a good proxy for juvenile recruitment) of either geckoes or skinks (Table 3).

3.6. Fecundity

The proportion of gravid female *D. conspicillatus* during spring/ summer was positively correlated with vegetation index (intercept

Table 3
Summary set of generalized linear models for juvenile recruitment.

Species	Model	LogL	k	ΔAIC_c	w_i	Dev (%)
C. schomburgkii	*C. leonhardii*+veg.	5.62	3	0	0.84	80.45
	C. leonhardii+*R. ornata*+veg.	5.72	4	3.64	0.14	80.69
C. leonhardii	*C. schomburgkii*	−14.37	2	0	0.38	26.13
	null	−16.49	1	1.55	0.17	0
C. regius	veg.	−11.29	2	0.00	0.43	41.48
	L. stenodactylum.prevyr+veg.	−9.77	3	0.27	0.38	52.89
L. stenodactylum	*C. regius.prevyr*	−6.92	2	0.00	0.50	33.36
	C. regius.prevyr+veg.	−6.26	3	1.87	0.19	38.94
R. ornata	den	−75.38	2	0	0.34	23.44
	null	−77.38	1	1.31	0.17	0
D. conspicillatus	null	−5.18	1	0	0.25	0
	R. ornata	−4.17	2	0.67	0.18	12.61

Note: Log likelihood (LogL), number of parameters (k), change in Akaike's Information Criterion, corrected for small sample size, compared to the best-ranked model (ΔAIC_c), model weights (w_i) and percentage explained deviance (Dev), for the statistical relationship between juvenile recruitment and total density in the previous year (*den*); immediate density of main interacting species (*species name*; see Methods) and their density in previous years (suffice = .*prevyr*); and vegetation condition (*veg.*). The null model (*null*) assumes a single mean rate across years. Note that only models with $w_i > 0.1$ are shown.

estimate = −0.30, standard error (SE) = SE 0.40; weighted model averaged coefficient = 1.01, (SE) = 0.41) (Table 5). By contrast, the proportion of gravid *L. stenodactylum* was positively related to extreme spring minimum temperatures (intercept estimate = −3.59, SE = 1.68; weighted model averaged coefficient = 0.63, SE = 0.25, Table 5). Fecundity in *R. ornata* was not adequately described by any of the candidate models: there was essentially equal support for the null model and low deviance explained.

4. Discussion

Densities of common lizards did not fluctuate synchronously as predicted if rainfall was the overarching driver of reptile assemblages in the arid zone. Density estimates for the six most abundant lizard species at an Australian arid zone site, fluctuated by up to a factor of six over a 15 year period. We found clear evidence that as well as rainfall, vegetation condition, seasonal extreme temperatures in the 12 months prior to sampling and inter-specific interactions are important additional determinants of key life-history traits (survival, fecundity and juvenile recruitment) for skink and gecko species at our study site. Replicated long-term studies in a range of habitats however are required to determine the degree to which these drivers influence other lizard assemblages and arid ecosystems.

Although resource availability and optimum temperatures for activity and reproduction in lizards have been widely recognised as playing a regulatory role in their population dynamics (see Pianka, 1986), this is the first long-term capture-mark-recapture field study to demonstrate that these factors operate differently between arid zone lizard species. Of particular note was the finding that peak densities of *C. leonhardii* coincided with a prolonged dry period, when vegetation condition and densities of two gecko species reached their lowest levels. In a six year study of lizard demographic dynamics in the western U.S. desert, Tinkle and Dunham (1986) also recorded that periods of high density of two congeneric lizard species did not necessarily coincide, which suggests that species-specific cues, like those effecting

Table 4
Weighted model averaged coefficients (and standard errors) for models describing year-to-year changes in the juvenile recruitment of *Ctenotus schomburgkii*, *Ctenotus regius* and *Lucasium stenodactylum* in response to vegetation condition (Veg.) and the immediate and lagged density (log(*n*)/ha) of potential interacting species (*species name*; see Methods); 'NA' is non-applicable.

Juvenile abundance		Model averaged coefficients				
Species		Intercept	Veg.	*C. leonhardii*	*L. stenodactylum*[a]	*C. regius*[a]
C. schomburgkii	Estimate	−0.99	0.23	0.56	NA	NA
	SE	0.72	0.06	0.15	NA	NA
C. regius	Estimate	0.58	0.44	NA	0.92	NA
	SE	0.49	0.14	NA	0.56	NA
L. stenodactylum	Estimate	0.21	0.25	NA	NA	0.24
	SE	0.50	0.23	NA	NA	0.10

[a] Relative abundance in previous year.

congeneric sympatric newts (Chadwick et al., 2006), are more influential on reptile and amphibian assemblages than has previously been recognised.

There was support for seasonal rainfall having a regulatory influence on the survival of four of the lizards analysed. Reproductive effort of several arid zone lizards has also been correlated with rainfall in the previous autumn or winter, which is a determinant of food availability and energy reserves during winter and early vitellogenesis (Zwiefel and Lowe, 1966; Parker and Pianka, 1975; Smith et al., 1995). In addition to the increase in resource availability, rainfall also drives an increase in vegetation structure and cover, which is considered a key determinant of Australian arid zone lizard assemblages (Read, 1995a; Letnic et al., 2004) and was influential in the recruitment models for *C. schomburgkii*, *C. regius* and *L. stenodactylum*, but not *C. leonhardii, D. conspicillatus* and *R. ornata* (Table 6). Therefore, our *a priori* hypothesis that productivity driven by rainfall is the primary driver of annual variability in Australian arid-zone reptile assemblages was only partially supported by this study.

Despite recognition that the thermal environment can profoundly affect lizard life histories (Adolph and Porter, 1993), the role of temperature, rather than just rainfall (Holmgren et al., 2006) in shaping the composition of arid herpetofauna has, until recently (Sinervo et al., 2010), been largely overlooked. For example, temperature variability was not recognised amongst fourteen propositions thought to govern Australian arid zone ecology (Morton et al., 2011). Yet we show that temperature explained the greatest amount of variation in fecundity rates for some lizard species (e.g., *L. stenodactylum)*; and may influence survival rates. The preferred body temperature and critical minimum temperatures of sympatric *Ctenotus* vary by at least 1 and 2 °C respectively (Bennett and John-Alder, 1986). Temperature also influences hatching rate and hatchling fitness (Packard and Packard, 1988; van

Table 5
Summary set of generalized linear models for fecundity among three species of gecko.

Species	Model	LogL	k	ΔAIC_c	w_i	Dev (%)
D. conspicillatus	*veg.*	−27.52	2	0.00	0.67	26.4
R. ornata	*veg.*	−43.15	2	0.00	0.27	9.6
	temp[summer min.]	−44.92	2	0.67	0.19	7.8
	null	−43.49	1	0.86	0.17	0.0
	temp[spring min.]	−43.82	2	1.35	0.14	6.0
L. stenodactylum	*temp[spring min.]*	−31.08	2	0.00	0.66	20.5
	null	−34.32	1	3.79	0.10	0.0

Note: Log likelihood (LogL), number of parameters (*k*), change in Akaike's Information Criterion, corrected for small sample size, compared to the best-ranked model (ΔAIC_c), model weights (*w_i*) and percentage explained deviance (Dev), for the relationship between proportion of gravid versus non-gravid mature females and environmental variables such as vegetation condition (*veg.*), average of the 20 coldest annual minimum temperatures for summer (*summer min*) and spring (*spring min*). Note that only models with $w_i > 0.1$ are shown.

Damme et al., 1992; Shine and Elphick, 2001), growth rate of juveniles, age at maturity and reproductive effort of lizards (Smith et al., 1995). Predicted changes in mean and extreme temperatures in the order of 3−7 °C (Suppiah et al. (2006)) would therefore likely drive considerable shifts in *L. stenodactylum* fecundity along with the competitive advantages of other central Australian lizard species with different thermal preferences.

We found evidence of relationships between IOD and both gecko recruitment and *C. leonhardii* survival. The cumulative influence of this regional climatic driver may therefore be more significant for these particular population parameters of desert lizards than variability in temperature or rainfall profiles alone, possibly due to interactions between rainfall, temperature, humidity and cloud cover. Furthermore, the greater influence of IOD on lizard population parameters than SOI suggests that, counter to studies further east in the Australian arid zone (Letnic et al., 2004; Vines, 2008), the Indian Ocean may have a greater influence than ENSO on the biota, as well as weather patterns (Ummenhoffer et al., 2009), of much of the Australian arid zone.

Likely surrogates for resource availability (vegetation condition and warm spring/autumn extreme minima) were key drivers of the percentage of gravid *L. stenodactylum* and *D. conspicillatus* respectively. However, periods of above-average rain in the arid zone, despite being an important determinant of increased survival, recruitment success (Table V, James, 1991b), resource availability and daily activity (Heatwole and Taylor, 1987), do not necessarily lead to consistent increases in abundance of arid zone lizards, due in part to variation in key life-history traits. For example, the short-lived *R. ornata* exhibits a relatively constant and high reproductive effort, as estimated by both percentage of gravid females and hatchlings captured, which were not correlated with any of the measured environmental factors. By contrast, other arid zone genera, including *Ctenotus*, either restrict investment in reproduction in dry years with low resource availability (Ballinger, 1977), or exhibit reduced survival in years of high reproductive effort (James, 1991a; Adolph and Porter, 1993; Read, 1998).

The marked annual variation in recruitment for *C. leonhardii* and *C. regius* in this study have also been recorded elsewhere for *Ctenotus*, including *C. leonhardii* (James, 1991a). Variability in reproductive output may be even greater in other *Ctenotus* populations, given that clutch size of *C. leonhardii* regularly reaches seven in the Great Victoria Desert (Pianka, 1969) but is typically only two at Olympic Dam (Read, 1998). Differing life-history traits and their response to different climate and environmental forces therefore seem to partly explain divergent density dynamics of sympatric lizards in a variable environment.

The lack of correlation between adult densities and juvenile recruitment the following year is counterintuitive if: 1) a greater number of adults were expected to infer higher reproductive potential; or 2) if high densities of adults were expected to usurp food or shelter resources and thus hinder recruitment of the next

Table 6
Main factors influencing the survival, recruitment and fecundity of three skinks (*Ctenotus schomburgkii*, *Ctenotus leonhardii* and *Ctenotus regius*) and three species of gecko (*Diplodactylus conspicillatus*, *Lucasium stenodactylum* and *Rhynchoedura ornata*) in arid Australia. The decision to include factors in the table is based on change in Akaike's Information Criterion, corrected for small sample size, compared to the best-ranked model ($\Delta AIC_c < 2$).

generation. In contrast, this result suggests that environmental and climatic factors were more important drivers of lizard recruitment than adult densities, which explains the dynamism of relative abundances of different lizard species and highlights the sensitivity of lizard assemblages to climatic and environmental changes. Modelled recruitment rates may have also been influenced by immigration or emigration of juveniles from the study site, although we assume that the climatic and environmental factors influencing recruitment would be consistent on and immediately adjacent to the unbounded study site. Positive correlation of *L. stenodactylum* recruitment with adult densities of *C. regius* in the previous year, and vice versa, may indicate that both species are responding to fluctuations in a common dietary item that was not an available predictor for the modelling. Experimental manipulation of food and other resources would likely be required to elucidate key population drivers in these cases, which highlights the difficulties in determining causation in dynamic and interacting faunal assemblages.

5. Conclusions

By analysing a 15-year multi-species capture-mark-recapture dataset, we have been able to clarify the relative contribution of climatic, environmental and competitive influences on lizard demography at an Australian arid zone site. A consistent finding was that annual variability of a number of species-specific climatic influences, including rainfall and temperature, and environmental variables such as vegetation condition and density of competitors, were typically stronger determinants of abundance than intraspecific factors such as adult density in the previous year. This result helps explain the dramatic and often asynchronous annual fluctuations in Australian lizard assemblages and implies that projected shifts in rainfall and temperature profiles due to global climate change will affect the density, relative abundance and perhaps distribution and status of some species The magnitude of the annual variability in lizard density at our study site highlights the importance of further studies of this kind to determine the generality of the findings and suggests that caution should be exercised if short-term lizard monitoring is used to monitor biodiversity impacts of deterministic anthropogenic land uses, such as mining impacts, grazing, or vegetation change, in arid ecosystems.

Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.actao.2011.09.006.

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