Oecologia (1999) 119:357–366

Christopher R. Dickman · Mike Letnic · Paul S. Mahon

Population dynamics of two species of dragon lizards in arid Australia: the effects of rainfall

Received: 11 September 1998 / Accepted: 10 February 1999

Abstract The population dynamics of two species of agamid (dragon) lizards were studied in the Simpson Desert, central Australia, over a period of 7 years, and modelled in relation to rainfall. Both species have annual life cycles, with adults predominating during the breeding season in spring and summer and juveniles predominating in other seasons. Within years, juvenile abundance in both species in autumn and winter was related most strongly to rainfall in the preceding summer and autumn. This pattern suggests that rainfall enhances survival, growth and possibly clutch size and hatching success. Between years, however, rainfall drove successional change in the dominant plant species in the study area, spinifex *Triodia basedowii*, causing in turn a shift in the relative abundance of the two species. Thus, the central netted dragon *Ctenophorus nuchalis* was most numerous in 1990 when vegetation cover was $<10\%$, but declined dramatically in abundance after heavy rainfall at the end of that year. In contrast, the military dragon *C. isolepis* achieved greatest abundance following heavy rains in the summers of 1990 and 1994, when spinifex cover increased to $>20\%$, and remained numerically dominant for much of the study. We suggest that drought-wet cycles periodically reverse the dominance of the two species of *Ctenophorus*, and perhaps of other lizard species also, thus enhancing local species diversity over time. Further long-term studies are needed to document the population dynamics of other species, and to identify the factors that influence them.

Key words Population dynamics · Dragons · Lizards · Arid zone · Diversity

C.R. Dickman (✉) · M. Letnic · P.S. Mahon
Institute of Wildlife Research and School of Biological Sciences
A08, University of Sydney,
NSW 2006, Australia
e-mail: cdickman@bio.usyd.edu.au,
Tel.: +61-2-93512318, Fax: +61-2-93514119

Introduction

Arid environments are often characterised by high spatial and temporal variation in the occurrence of rainfall. Because rainfall is a stimulus for increased primary productivity (Rosenzweig 1968), animal activity in arid environments can in turn be expected to be spatially and temporally variable. Desert vertebrates display a wide range of ecological and physiological adaptations that allow growth and successful reproduction in such environments. Mobile vertebrates such as birds and some mammals can move long distances to escape drought-struck areas (Schodde 1982; Davies 1984; Dickman et al. 1995), while sedentary species may reduce activity during dry periods and seek shelter in moist refugia or deep underground (Heatwole 1984; Cloudsley-Thompson 1991). Some sedentary species possess physiological mechanisms to reduce water loss and metabolic rate, and may postpone reproduction for long periods until favourable conditions return (Predavec and Dickman 1993). Others show considerable flexibility in diet, maintaining activity by opportunistically exploiting diverse food resources (Reichman et al. 1979; Murray and Dickman 1994).

Lizards are considered to be particularly well adapted to arid environments because of their low energy and water requirements (Pough 1980; Bradshaw 1986, 1997), ability to aestivate during periods unfavourable for activity, dietary opportunism and, in some species, ability to store fat (Case 1976; Whitford and Creusere 1977; Pianka 1986; James 1991a, 1991b). Most species studied appear to be seasonal breeders, although exceptions are known (Saint Girons 1984; Robinson 1990). Desert lizards also display a diverse set of physiologically conservative life history traits that encompass the range of predictions of the r-K selection model (Pianka 1970, 1986), and beyond (Congdon et al. 1978; Dunham et al. 1989). Species with annual life cycles are characterised by rapid maturity, production of multiple clutches and turnover of the population within 1 year (Tinkle 1967; Orr et al. 1979). Given their high investment in reproduction and short life span, annual lizards are considered to be relatively r-selected and characteristic of variable, unpredictable environments (Bradshaw 1986; Pianka 1986). In contrast, perennial lizards often exhibit slower or more variable growth and reproduction and have relatively stable populations; such species may be positioned toward the K-selected end of the continuum (Pianka 1970, 1986).

In arid Australia, spatial and temporal variation in the occurrence and intensity of rainfall can be extreme (Gibbs 1969; Stafford Smith and Morton 1990). This may have correspondingly dramatic effects on population dynamics and the intensity and timing of reproduction in both annual and perennial lizard species (e.g. How et al. 1986, 1990; Henle 1990, 1991; James 1991a, 1991b). In a particularly instructive long-term study, Bradshaw et al. (1991) showed that the timing of reproduction of an annual species of dragon (agamid) lizard, *Ctenophorus nuchalis*, is dictated primarily by rainfall. This species breeds predictably after winter rains in the southern part of its range, and in late summer following cyclonic rains in the Pilbara region further north. It may also breed in spring in the latter region, but only if winter rain has been substantial. In contrast to the flexible breeding of *C. nuchalis*, sympatric *C. caudicinctus* breeds only in late summer after cyclonic rain, but invests greater per capita reproductive effort (Bradshaw et al. 1991). The population dynamics of these species differ markedly between areas and years (Bradshaw 1986; Saint Girons et al. 1992). Long-term patterns in the abundance of *Ctenophorus* species and other arid-zone agamids are probably also related to the seral stage of vegetation that is recovering after fire or drought (Masters 1996). However, habitat effects on demography generally remain poorly known.

Despite recognition of the probable effects of rainfall on arid-zone lizard species and the importance of long-term studies for revealing the extent of demographic variation (Dunham et al. 1989; Pianka 1996), little relevant work has been carried out (cf. Bradshaw et al. 1991). In the present paper, we describe the population dynamics of two species of dragon lizards (family Agamidae), the central netted dragon *C. nuchalis* and military dragon *C. isolepis*, from a study site in the Simpson Desert of central Australia, over a 7-year study period. Our specific aim is to model the population dynamics of the two species in relation to rainfall and change in vegetation cover. Like *C. nuchalis*, *C. isolepis* appears to be an annual species (Storr 1965; Pianka 1971a). However, while *C. nuchalis* prefers open sites, *C. isolepis* usually occupies hummock grass or other vegetation and is seldom found far from cover (Gibson and Cole 1988; Downey and Dickman 1993).

Materials and methods

Study area

The study area was located on Ethabuka cattle station in the north-eastern Simpson Desert, south-western Queensland (23°46′S, 138°28′E). The dominant landforms within the study area are parallel sandridges between 8–10 m in height, running in a NNW–SSE direction (Purdie 1984). The dune slopes and sandy interdune corridors support hummock grassland dominated by *Triodia basedowii*. Shrubs, including *Grevillea stenobotrya*, *Eremophila* spp., *Acacia ligulata* and *Dodonaea angustissima*, are common in these areas. Vegetation on dune crests is relatively sparse and dominated by shrubs, particularly *Crotalaria* spp., *Sida* spp. and *G. stenobotrya* (Dickman et al. 1995), and following rain many ephemeral herbs and forbs are present. Plains, or swales, between sand dunes have clay soils with vegetation dominated by the tree *A. cambagei* (gidyea), forbs and short grasses.

The Simpson Desert is classified as a hot desert. The study area lies between the 150-mm and 100-mm median annual rainfall isopleths (Purdie 1984). The nearest weather stations to the study area, at Sandringham, Marion Downs and Glenormiston, have average rainfalls of 172 mm (n = 40 years), 196 mm (n = 82 years) and 203 mm (n = 95 years), respectively. In the northern part of the desert there is a pronounced wet season with most rainfall occurring between December and March; however, the annual occurrence and intensity of rainfall is unpredictable (cf. Morton 1982). The mean annual temperature is 21–23°C with maxima of 46–49°C in summer and minima of −6°C in winter (Purdie 1984).

Trapping

Animals were live trapped on twelve study grids. Grids were 0.5–2 km apart, with each grid comprising six lines of six pitfall traps spaced 20 m apart and covering 1 ha. One edge of each grid was positioned along a dune crest, the opposite boundary being 100 m away in the swale. Pitfall traps consisted of a 5-m drift fence made of aluminium flywire, positioned over a length of PVC pipe (16 cm diameter, 60 cm deep), buried flush with the ground (Friend et al. 1989). Flywire was placed underneath the traps to prevent animals from escaping from the bottom of the traps. To prevent accidental capture of animals, lids were placed on traps when not in use.

On capture, individuals were given a unique toe clip for identification, and the following measurements were taken: snout-vent length (SVL) and total length to the nearest millimetre, jaw length to the nearest 0.1 mm, and mass to the nearest 0.1 g. Where possible the sex of animals was determined, their breeding condition observed and the presence or absence of a hatchling scar noted. Hatchlings had a SVL $<$ 30 mm, juveniles were $\geq$ 30 mm but $\leq$ 55 mm, while adults were characterised by SVLs $>$ 55 mm (C.R.Dickman and M.Letnic, unpublished data).

Trapping was conducted approximately six times per year at about 2-month intervals, between March 1990 and November 1996, with grids being checked in the morning and sometimes in the afternoon for 2–4 consecutive days. The grids trapped and the length of trap sessions varied from session to session. Trap effort was standardised as captures per grid per day. Standardised trap data are used for calculation of and comparison of the mean trapping rate for each season, where seasons were defined as: autumn, March–May; winter, June–August; spring, September–October; summer: November–February. Mean values for each season were used for regression analyses.

Rainfall

Monthly cumulative rainfall totals were obtained for the two nearest rain stations to the study area, Glenormiston (22°55′S, 138°49′E) and Sandringham (24°03′S, 138°04′E), approximately 95 km and 75 km from the study site, respectively (Bureau of

Meteorology, Canberra). Total rainfall within each season was then estimated by taking the average value for these weather stations.

Vegetation cover and lizard habitat use

Assessments of the ground covered by hummock grass or spinifex, *T. basedowii*, were taken each season on five representative grids. Assessments were made by estimating the area covered by spinifex as a percentage of a 2.5-m-radius circle centred on a pitfall trap station. Estimates were taken at six trap stations per grid, representing one station from each row of traps within a grid. A measure of the spinifex cover on each grid was calculated as the mean of the six measurements.

To examine the habitat use of the two lizard species, the number of captures in each trap row was then compared against an expected frequency of no preference (i.e. the number of captures in each row was equal) and tested using the *G*-test. Habitats were broadly categorised as dune top (row 1), dune side (rows 2 and 3) and swale (rows 4–6).

Statistical analyses

Linear multiple-regression models were used to examine time series plots of lizard capture rates in relation to season, rainfall, and *Triodia* cover on the study grids. A stepwise procedure was used to enter variables into predictive models on the strength of their partial correlation coefficients. Variables were included in models only if they were individually significant ($P < 0.05$) or if their inclusion provided a greater than 5% increase of the variance in capture rate explained by the overall model. Adults and juveniles were analysed separately and together.

A number of rainfall-related variables were trialed for regression analyses. These included total rainfall in the preceding season and for up to all four seasons in the previous year, rainfall that fell separately in the preceding autumn, winter, spring and summer, and the cumulative seasonal rainfall residual (Sutherland et al. 1991) with a 0.8 exponential decay function to accommodate the skewed distribution of seasonal rainfall around the means (Dickman et al. 1999). All variables provided similar results both in terms of variance in lizard capture rate explained and the predictive variables included in the models. Therefore, given the similarity between models, only the analyses including rainfall in the separate specified seasons are presented in this paper.

The annual life cycle of *C. isolepis* and *C. nuchalis* results in structured populations characteristic of each season (Storr 1965; Pianka 1971a; Bradshaw 1981), with adults predominating in spring and summer populations, while juveniles and subadults are predominant in autumn and winter populations. Thus, in order to partition variation between seasonal effects and the effects of variable rainfall and vegetation cover, seasons were entered into the regression analyses as binary variables. To do this, one season was identified as the base season, with changes in lizard abundance in the other seasons measured with respect to this base season (Mattikallia 1996). Seasons were thus represented in the data as dummy variables to represent seasons other than the base season.

Prior to constructing stepwise models, simple linear regressions were run of lizard capture rates against rainfall and cover variables. Analyses of residuals indicated no need for data transformations, so that original values of variables are used throughout. In addition, we note that although trapping data suffer from lack of temporal independence, analyses presented here are used purely as descriptive tools and not as tests of hypotheses.

Results

Trapping

Between March 1990 and November 1996 there were 581 and 96 captures of *C. isolepis* and *C. nuchalis*, respectively, over 1208 grid days. Recapture rates for both species were low, with only 34 *C. isolepis* and 3 *C. nuchalis* being recaptured between trapping sessions. Half of the recaptures of *C. isolepis* were made within 4 months of the initial capture, with only 2 at intervals of greater than 12 months. Recaptures of *C. nuchalis* took place at intervals of 2, 6 and 7 months, respectively. Given the low recapture rates, no population estimates could be made, and therefore population indices are presented based on direct enumeration of individuals actually caught.

Habitat use

Over the entire period of the study, the capture rate of *C. isolepis* was higher in swale than in dune top or dune side habitats ($G = 37.58$, $df = 5$, $P < 0.001$), whereas *C. nuchalis* was captured evenly across all trap rows ($G = 7.75$, $df = 5$, P n.s. Fig. 1). Spinifex cover was

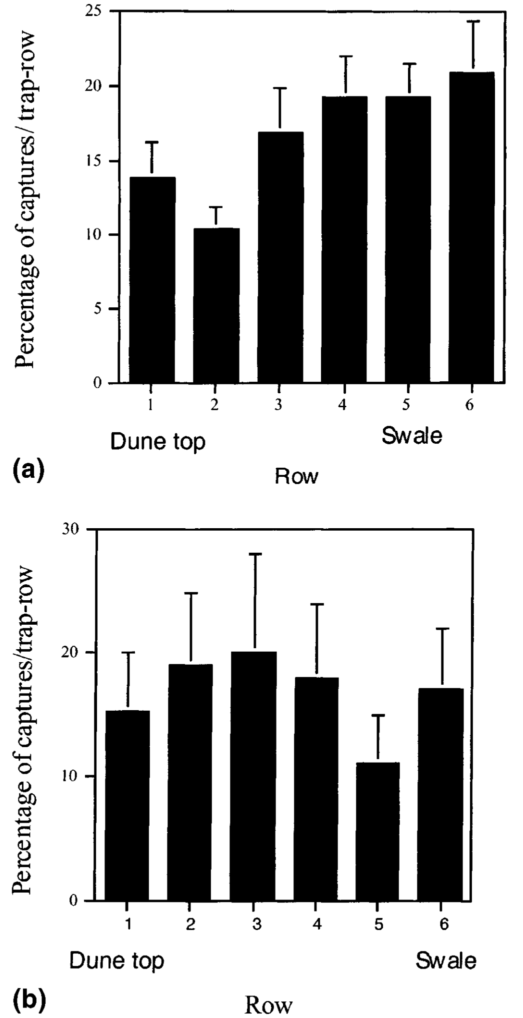


Fig. 1 Habitat use by dune topography for *Ctenophorus isolepis* (**a**) and *C. nuchalis* (**b**). Error bars represent ± 1 SE, and *Row* indicates the position of pitfall trap rows from dune top (*1*) through dune side (*2, 3*) to swale (*4–6*)

greatest in the swales and less on the dune tops and dune sides, and also less in 1990 than towards the end of the study in 1995 (Fig. 2).

Population dynamics: long-term patterns

The increased cover of *T. basedowii* between 1990 and 1996 can be attributed to growth stimulated initially by the exceptionally high rainfall received in the summer of 1990 and, later, to growth following heavy rainfall in the summer of 1994 (Fig. 3). Rainfall was highest in summer and least in winter in most years. However, the timing and intensity of rainfalls varied greatly over the study period (Fig. 3).

Plots of abundance of adult and juvenile *C. isolepis* and *C. nuchalis* showed seasonal trends, with adults being dominant in spring and summer populations and juveniles dominant in autumn and winter (Figs. 4, 5).

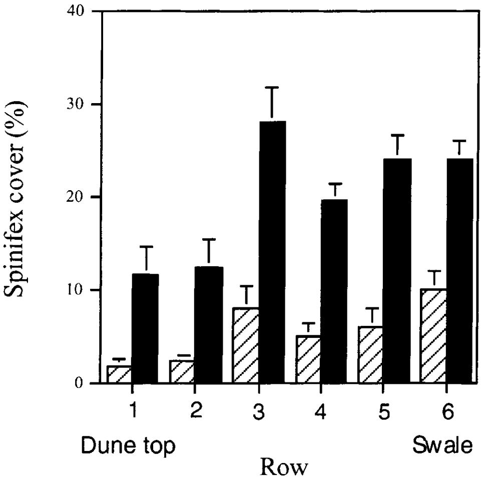


Fig. 2 Spinifex cover in 1990 (*cross hatched*) and 1995 (*filled*) on each trap row. Error bars represent ±1 SE

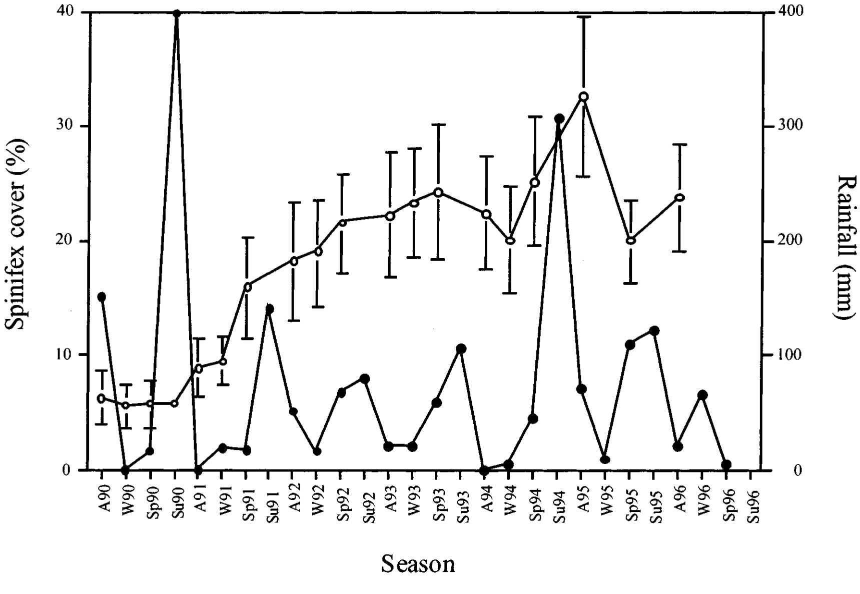
The abundance of *C. isolepis* showed a marked increase following heavy rainfall during the wet season of 1990. Thereafter, the population density of *C. isolepis* remained relatively stable until 1994, when heavy wet-season rains again appeared to result in a population increase in the following year. In 1996, the population size decreased to a level similar to that prior to 1995 (Fig. 4). The population density of *C. nuchalis* decreased dramatically over the duration of the study, its density being greatest in 1990, but decreasing rapidly during 1991 and 1992. Very few or no individuals were captured in 1993 and 1994, and low densities were observed in 1995 and 1996 (Fig. 5).

Regression analyses

Dummy variables representing each season were used to account for seasonal variation in lizard abundance. The base seasons for adult, juvenile and total abundance were autumn, spring and winter, respectively and do not appear in the models.

Seasonal variables helped to explain much of the variation in the abundance of adult and juvenile *C. isolepis* and *C. nuchalis*. This reflects the seasonal occurrence of adults and juveniles arising from the annual life history strategy of these species. The fitted model for juvenile *C. isolepis* was the most successful in explaining variation in capture rates, with 65% of variation explained by the model (Table 1; Fig. 6). Juveniles were most abundant in autumn and winter, respectively, and were correlated positively with spinifex cover and rainfall in the preceding summer (Table 1). The density of adults was greatest in spring and summer and correlated positively with spinifex cover (Table 1). The total abundance of *C. isolepis* was generally greatest in summer and correlated positively with spinifex cover, summer and autumn rainfall (Table 1).

Fig. 3 Rainfall (*closed symbols*) and spinifex cover (*open symbols*) over the study period. Error bars represent ±1 SE (*A* autumn, *W* winter, *Sp* spring, *Su* summer)



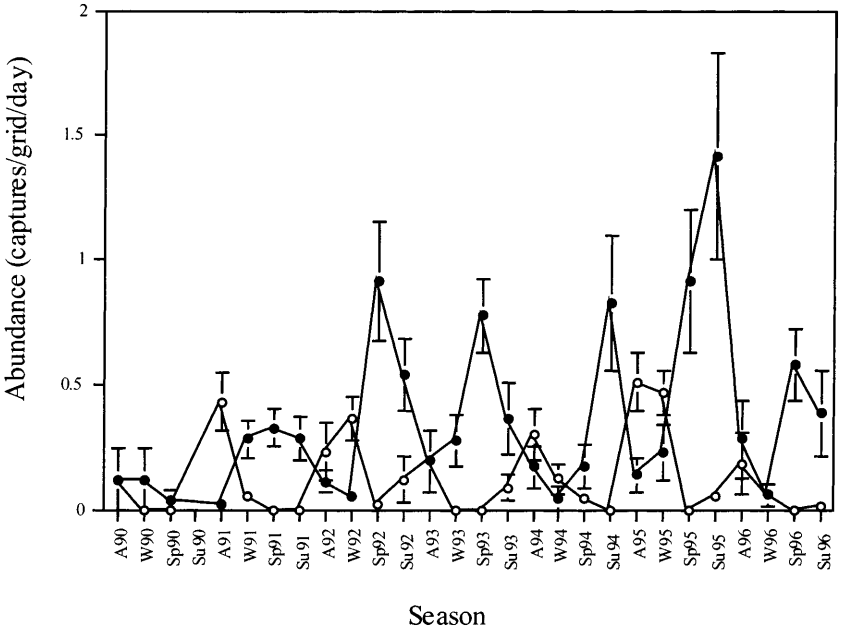


Fig. 4 Abundance of adult (*closed symbols*) and juvenile (*open symbols*) *C. isolepis* over the study period expressed as mean captures per grid per day. Error bars represent ±1 SE (*A* autumn, *W* winter, *Sp* spring, *Su* summer)

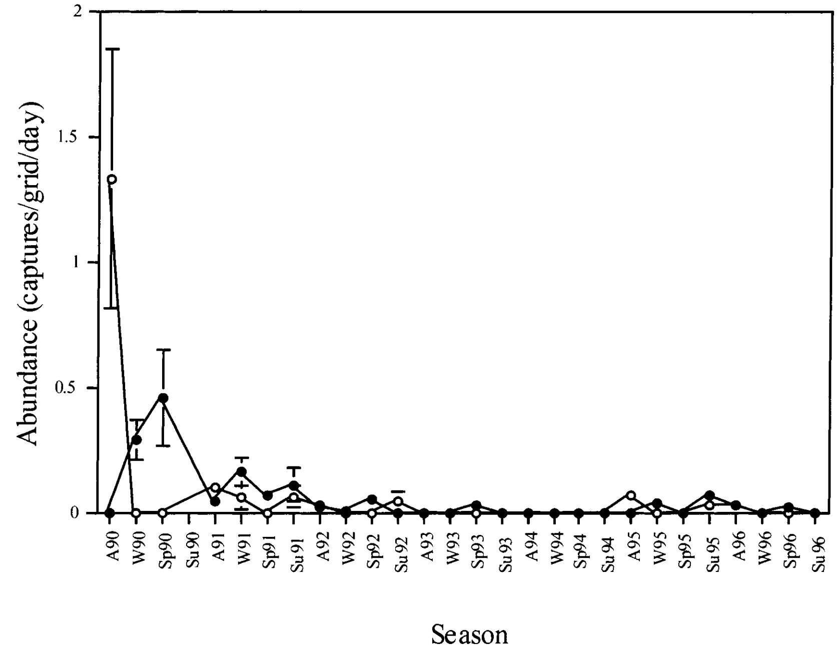


Fig. 5 Abundance of adult (*closed symbols*) and juvenile (*open symbols*) *C. nuchalis* over the study period expressed as mean captures per grid per day. Error bars represent ±1 SE (*A* autumn, *W* winter, *Sp* spring, *Su* summer)

The abundances of adult and juvenile *C. nuchalis* were correlated negatively with spinifex cover (Table 1). Juveniles were most abundant in autumn, while adult abundance was correlated positively with autumn rainfall (Table 1).

Discussion

Our results support previous work suggesting that both *C. isolepis* (Storr 1965; Pianka 1971a) and *C. nuchalis* (Bradshaw 1986) have predominantly annual life cycles. This was shown particularly by the predictable domination of adults in spring and summer populations and juveniles in autumn and winter, but also by the very small percentages of animals recaptured at intervals of more than a year. In other work (C.R. Dickman, M. Letnic, G.H. McNaught, unpublished data), we have confirmed that an almost complete replacement of previous-year adults takes place by late autumn, with juveniles attaining sexual maturity after winter at 5–6 months of age. Several further life history traits are associated with the rapid annual turnover of *C. isolepis*, including small adult body size (maximum observed SVL = 72 mm), production of several (two to five) eggs per clutch and double clutching (Pianka 1971a). Similar

Table 1 Stepwise multiple-regression equations of capture rates of *Ctenophorus isolepis* and *C. nuchalis* against season, vegetation cover and rainfall for all seasons between autumn 1990 and summer 1996. Significant seasonal patterns in abundance are shown by the presence of seasonal dummy variables. Equations show rainfall in separate specified seasons for up to 1 year previously (*cover* is percentage cover of spinifex, *Triodia basedowii*; *aut*, *win*, *sp* and *sum* are dummy variables for autumn, winter, spring and summer, respectively; *autR* and *sumR* are previous autumn and summer rain, respectively

Variable	Equation	R^2 (%)	F
C. isolepis			
Adult	$y = 0.156 + 0.374\ \text{sp} + 0.450\ \text{sum} + 0.011\ \text{cover}$	46.4	8.55**
Juvenile	$y = -0.191 + 0.271\ \text{aut} + 0.007\ \text{cover} + 0.0003\ \text{sumR} + 0.142\ \text{win}$	65.1	10.24***
Total	$y = -0.245 + 0.023\ \text{cover} + 0.206\ \text{sum} + 0.002\ \text{autR} + 0.0007\ \text{sumR}$	38.8	3.64*
C. nuchalis			
Adult	$y = 0.152 - 0.0067\ \text{cover} + 0.0008\ \text{autR}$	50.1	12.05**
Juvenile	$y = 0.276 + 0.201\ \text{aut} - 0.013\ \text{cover}$	28.2	4.72*
Total	$y = 0.568 + 0.211\ \text{aut} - 0.026\ \text{cover}$	38.0	7.48*

*$P < 0.05$; **$P < 0.001$; ***$P < 0.0001$

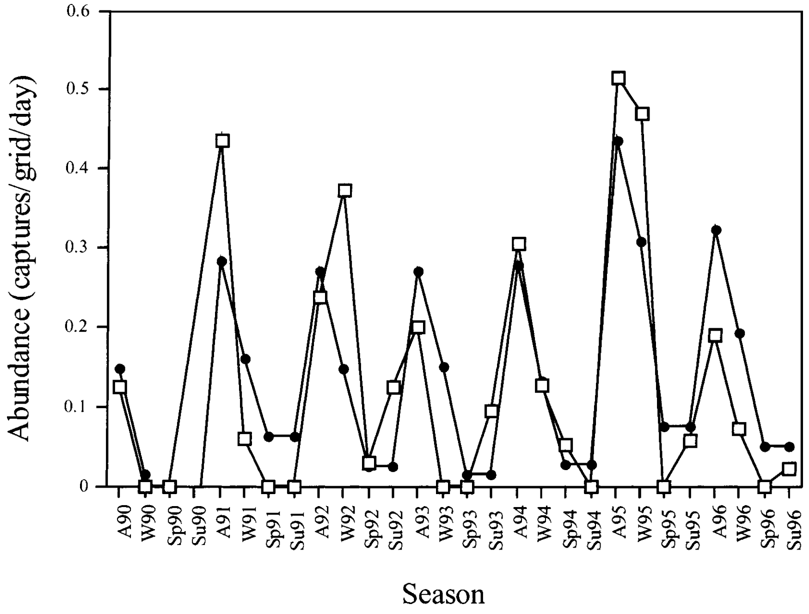


Fig. 6 Actual values (*open symbols*) and fitted values (*closed symbols*) estimated using stepwise multiple regression for juvenile *C. isolepis*. For the fitted model R^2 = 65.1% and y = −0.191 + 0.271 autumn + 0.007 spinifex cover + 0.0003 summer rain + 0.142 winter

traits appear to be characteristic also of other *Ctenophorus* species, including *C. fordi* (Cogger 1974) and *C. pictus* (Henle 1989), and other predominantly annual lizards in Israel and North America (Tinkle 1967; Orr et al. 1979).

Despite similarity in the timing of major demographic events, numbers of *C. nuchalis* declined dramatically over the course of the study whereas those of *C. isolepis* increased. These long-term fluctuations in abundance are most likely to have been driven directly by rainfall, and by the interaction of rainfall with vegetation cover and food resources. For *C. nuchalis*, capture rates were associated most consistently, and negatively, with vegetation cover; the lowest capture rates followed the growth of spinifex that was stimulated by the heavy rainfall of summer 1990. It is conceivable that heavy rainfall had some direct effect on *C. nuchalis*, perhaps drowning animals in floodwaters on the swales, but if this was so, the effect was manifested only in the rains of summer 1990 and not in those of other years. Several species of arid-zone lizards appear to be little affected by short-term flooding, climbing shrubs to avoid surface water (Henle 1996). Furthermore, autumn capture rates of *C. nuchalis*, especially of juveniles, were associated positively with autumn rains (Table 1). Catchability may also increase following rainfall. More importantly, such rainfall may improve conditions for incubation and hatching of late-season clutches, and may further promote a flush in food availability that speeds growth and increases survival in juveniles (Haynes 1996). In the North American iguanid *Uta stansburiana*, artificial watering to simulate rainfall elevated the biomass of food resources and allowed females to produce larger clutches than "dry" control females (James and Whitford 1994). It is possible that rainfall increased clutch sizes in the present study also, but we have no data to evaluate this.

It is further conceivable that heavy rainfall impacted indirectly on *C. nuchalis* by allowing population increases of lizard predators. The number of feral cats, *Felis catus*, increased in the study area in 1991 and 1992 following the heavy rainfall of summer 1990, while evidence of red fox, *Vulpes vulpes*, activity was detected for the first time in mid 1991 (Dickman 1996a; Mahon 1999). However, strong predatory impact is unlikely. While both species of predators eat dragon lizards, *Ctenophorus* spp. comprise a minor part of the diet (<5% by volume; Dickman 1996b; Mahon 1999). Furthermore, populations of *C. nuchalis* remained low from 1991 until the end of the study, even though the numbers of foxes and cats dwindled from 1993 (Mahon 1999). No formal census was made of potential avian predators of dragon lizards such as brown falcons, *Falco berigora*, and Australian kestrels, *Falco cenchroides*. However, casual observations (C.R. Dickman, personal observation) suggested no dramatic increases following the 1990 summer rains that might correlate with the decline in numbers of *C. nuchalis*.

The negative effect of increased spinifex cover on *C. nuchalis* can be interpreted largely in terms of the thermoregulatory and shelter requirements of this species. *C. nuchalis* is mostly terrestrial and constructs burrows within hillocks such as those formed by dead *Triodia* hummocks, but often basks on elevated perches close to burrow entrances (C.R. Dickman, personal observation). An increase in spinifex cover such as that observed during the study period may have resulted in reduced availability of burrow sites and precluded access to perches. In addition, *C. nuchalis* takes relatively many large invertebrates in the diet; such prey are available primarily in open microhabitats and bare sand (Fisher and Dickman 1993), and would thus have been reduced by spinifex growth.

For *C. isolepis*, abundance was associated strongly with vegetation cover and rainfall; there was no evidence that numbers were correlated with predator activity. The lowest capture rates in 1990 coincided with spinifex cover of only 6–7%, but by 1992 when cover reached a threshold of 20% (Fig. 3), juvenile and especially adult numbers remained remarkably stable. In contrast to its larger congener, *C. isolepis* appears to be strictly terrestrial and uses the shade of spinifex hummocks in its thermoregulatory behaviour (Losos 1987, 1988); shelter is usually sought under spinifex, although burrows are constructed in open sand among hummocks during summer. Strong correlations of autumn and winter captures of juveniles with preceding summer rainfall suggest beneficial effects of rain on both hatching success and juvenile survival. In addition to maintaining the cover of spinifex, high wet-season rainfall stimulates production of seeds from annual and perennial grasses and shrubs (Dickman et al. 1999). This in turn appears to increase autumn and winter abundance of seed-harvesting ants (Reid 1995). Since small ants, including many harvester species, form the bulk of the diet of juvenile and adult *C. isolepis* (Pianka 1971a, 1986; unpublished data), summer rainfall may be crucial for promoting juvenile survival and growth.

If these interpretations are correct, both long-term abundance and inter-annual cycles of the two *Ctenophorus* species are driven by rainfall. Within years, rain enhances survival, growth and possibly hatching of both species. Following periods of above-average rainfall that have promoted a dense cover of spinifex and other ground vegetation, *C. isolepis* is likely to be the dominant species. In contrast, following drought when spinifex has died back (Jacobs 1984) and ground cover is sparse (<10%), *C. nuchalis* can be expected to predominate. To test these expectations we plotted long-term rainfall records from Glenormiston (Fig. 7), and reviewed collection data pre-1990 on both *Ctenophorus* species from the Simpson Desert from literature sources. In 1939, an average rainfall year following severe drought, Kinghorn (1945) recorded many specimens of *C. nuchalis* from across the Simpson Desert, but obtained only five *C. isolepis* from near the Hay River.

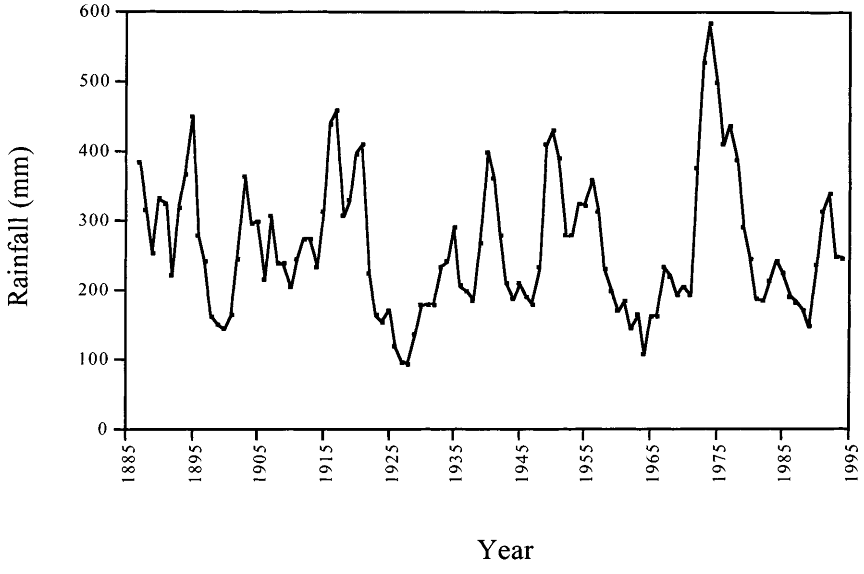


Fig. 7 Three-point moving average annual rainfall for the Glenormiston rain station for 95 years of records

In contrast, in a very wet period in the mid 1970s, Bolton et al. (1977) reported *C. isolepis* to be abundant in the western Simpson and *C. nuchalis* to be uncommon. Finally, in low-rainfall years of the early to mid 1980s, Atherton et al. (1985) reported *C. isolepis* to be more restricted than *C. nuchalis* in the eastern Simpson Desert and sighted the former species less frequently. Although limited, these findings conform with our prediction that *C. isolepis* is the dominant species during pluvial periods whereas *C. nuchalis* predominates during drought. In a similar context, Masters (1996) noted that *C. nuchalis* is an early recoloniser following fire, and that *C. isolepis* recolonises later when vegetation cover has been restored.

The dramatic effects of rainfall on *Ctenophorus* spp. are paralleled in other taxa. Working in the same study area, Predavec (1994) showed that the native rodents *Notomys alexis* and *Pseudomys hermannsburgensis* erupted after the heavy rainfall of summer 1990 and again after heavy rainfall the following summer, with the latter species showing strong temporal and spatial correlations with seed availability. A further eruptive species, *Rattus villosissimus*, was present at Ethabuka from mid 1991 until late 1992, as was a specialist rat predator, the letter-winged kite *Elanus scriptus* (Predavec and Dickman 1994). Rainfall has been documented to drive population fluctuations in many other taxa throughout arid Australia (Newsome and Corbett 1975; Schodde 1982; Dickman 1993; Dickman et al. 1999) and in deserts elsewhere (e.g. Brown and Heske 1990; Meserve et al. 1995). In most studies, population fluctuations after rain have been interpreted as responses to changes in levels of resources such as food and shelter. However, biotic factors such as competition, predation, and facilitation may also be important in driving the dynamics of some species populations (Thompson et al. 1991; Heske et al. 1994; Meserve et al. 1996).

Although temporal shifts in the dominance of each species of *Ctenophorus* are most likely responses to rainfall-induced changes in vegetation cover, the two species could potentially interact directly through competition or predation. Hutchinson (1961) suggested that the competitive abilities of species could be altered by changing environmental conditions, and that this could promote coexistence; inverse numerical relationships have since been used as potential indicators of competition in diverse taxa (e.g. Grant 1978; Dickman 1984). In the present study, however, competition seems unlikely. The two species exploit different microhabitats, with *C. isolepis* preferring sites in dune swales with denser vegetation and more compacted sand, and *C.nuchalis* preferring open sites on dune tops and swales (Fig. 1; Gibson and Cole 1988; Downey and Dickman 1993). Both species include arthropods in their diet, but *C. isolepis* is an ant specialist whereas *C. nuchalis* takes prey from the spectrum that is available, in addition to some plant material (Pianka 1971b, 1986). Moreover, there is no evidence of habitat or dietary shift between sympatry and allopatry in the two species in western Queensland (C.R. Dickman, personal observation), and thus little indication that these dragon lizards interact directly in any way.

Point-sample or alpha diversity of lizards in arid Australia is high relative to that in other world deserts (Pianka 1986, 1994). Hypotheses accounting for this diversity have been based on the breadth or abundance of available food resources (Morton and James 1988), on the diversity of habitats and microhabitats (James 1994; Read 1995), and on combinations of ecological and historical factors (Pianka 1989, 1994). More recently, it has become clear that the abundance of many species changes dramatically over time (Pianka 1996; Smith et al. 1997), causing long-term point-sample counts of species to increase. Changes in abundance are known to occur in response to fire-driven changes in vegetation succession (Masters 1996; Pianka 1996). Our results on *Ctenophorus* dragon lizards and those of Haynes (1996) on *Ctenotus* skinks suggest that drought-wet cycles may also contribute to increasing point-sample diversity via their effects on vegetation cover (Fatchen and Barker 1979; Jacobs 1984) or even levels of groundwater (Braithwaite and Muller 1997). We conclude by echoing Pianka's (1996) call for further long-term studies to document fluctuating species populations and suggest further that experiments be undertaken to disentangle the contributions of rainfall, food and cover resources to local abundance.

Acknowledgements We thank D. and P. Smith for hospitality and access to the study site at Ethabuka, G.H. McNaught, F.J. Qualls and numerous volunteers for assistance in the field, and Professors S.D. Bradshaw and R. Shine, and P. Harlow for providing critical comments on the manuscript. The research was funded by the Australian Research Council.

References

Atherton RG, Gordon G, Porter G, Reimer DS (1985) Fauna survey of the Diamantina Region, south-west Queensland. Queensland National Parks and Wildlife Service, Brisbane

Bolton BL, Latz PK, Gillam MW (1977) Simpson Desert: a proposal for a reserve. Conservation Commission of the Northern Territory, Alice Springs

Bradshaw SD (1981) Ecophysiology of Australian desert reptiles: studies on the genus *Amphibolurus*. In: Keast A (ed) Ecological biogeography of Australia, vol 2. Junk, The Hague, pp 1394–1434

Bradshaw SD (1986) Ecophysiology of desert reptiles. Academic Press, Sydney

Bradshaw SD (1997) Homeostasis in desert reptiles. Springer, Berlin Heidelberg New York

Bradshaw SD, Saint Girons H, Bradshaw FJ (1991) Patterns of breeding in two species of agamid lizards in the arid subtropical Pilbara region of Western Australia. Gen Comp Endocrinol 82:407–424

Braithwaite RW, Muller WJ (1997) Rainfall, groundwater and refuges: predicting extinctions of Australian tropical mammal species. Aust J Ecol 22:57–67

Brown JH, Heske EJ (1990) Temporal changes in a Chihuahuan Desert rodent community. Oikos 59:290–302

Case T (1976) Seasonal aspects of thermoregulatory behavior in the chuckwalla, *Sauromalus obesus* (Reptilia, Lacertilia, Scincidae). J Herpetol 12:428–429

Cloudsley-Thompson JL (1991) Ecophysiology of desert arthropods and reptiles. Springer, Berlin Heidelberg New York

Cogger HG (1974) Thermal relations of the mallee dragon *Amphibolurus fordi* (Lacertilia: Agamidae). Aust J Zool 22:319–339

Congdon JD, Vitt LJ, Hadley NF (1978) Parental investment: comparative reproductive energetics in bisexual and unisexual lizards, genus *Cnemidophorus*. Am Nat 112:509–521

Davies SJJF (1984) Nomadism as a response to desert conditions in Australia. J Arid Environ 7:183–195

Dickman CR (1984) Competition and coexistence among the small marsupials of Australia and New Guinea. Acta Zool Fenn 172:27–31

Dickman CR (1993) The biology and management of native rodents of the arid zone in New South Wales. New South Wales Natl Parks Wildl Serv Spec Manage Rep 12:1–149

Dickman CR (1996a) Incorporating science into recovery planning for threatened species. In: Stephens S, Maxwell S (eds) Back from the brink: refining the threatened species recovery process. Surrey Beatty, Sydney, pp 63–73

Dickman CR (1996b) Overview of the impacts of feral cats on Australian native fauna. Australian Nature Conservation Agency, Canberra

Dickman CR, Predavec M, Downey FJ (1995) Long-range movements of small mammals in arid Australia: implications for land management. J Arid Environ 31:441–452

Dickman CR, Mahon PS, Masters P, Gibson DF (1999) Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. Wildl Res

Downey FJ, Dickman CR (1993) Macro- and microhabitat relationships among lizards of a sandridge desert in central Australia. In: Lunney D, Ayers D (eds) Herpetology in Australia: a diverse discipline. Royal Zoological Society of New South Wales, Mosman, pp 133–138

Dunham AE, Grant BW, Overall KL (1989) Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiol Zool 62:335–355

Fatchen TJ, Barker S (1979) Cyclic vegetation pattern in the southern Simpson Desert. Trans Roy Soc South Aust 103:113–121

Fisher DO, Dickman CR (1993) Diets of insectivorous marsupials in arid Australia: selection for prey type, size or hardness? J Arid Environ 25:397–410

Friend GR, Smith GT, Mitchell DS, Dickman CR (1989) Influence of pitfall and drift fence design on capture rates of small vertebrates in semi-arid habitats of Western Australia. Aust Wildl Res 16:1–10

Gibbs WJ (1969) Meteorology and climatology. In: Slayter RO, Perry RA (eds) Arid lands of Australia. Australian National University Press, Canberra, pp 33–54

Gibson DF, Cole JR (1988) A biological survey of the northern Simpson Desert. Conserv Commission Northern Territory Tech Rep 40:1–205

Grant PR (1978) Competition between species of small mammals. In: Snyder DP (ed) Populations of small mammals under natural conditions. Pymatuning Laboratory of Ecology, University of Pittsburg, Linesville, pp 38–51

Haynes RS (1996) Resource partitioning and demography of twelve sympatric skinks (*Ctenotus*) in the Simpson Desert. Thesis, University of Sydney, Sydney

Heatwole H (1984) Adaptations of amphibians to aridity. In: Cogger HG, Cameron EE (eds) Arid Australia. Australian Museum, Sydney, pp 177–222

Henle K (1989) Ecological segregation in an assemblage of diurnal lizards in arid Australia. Acta Oecol Gen 10:19–35

Henle K (1990) Population ecology and life history of three terrestrial geckoes in arid Australia. Copeia 1990:759–781

Henle K (1991) Life history patterns in lizards of the arid and semiarid zone of Australia. Oecologia 88:347–358

Henle K (1996) Herpetological observations in Sturt National Park, northwestern New South Wales, with a comment on *Ctenotus uber* and *C. astarte*. Herpetofauna 26:12–25

Heske EJ, Brown JH, Mistry S (1994) Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. Ecology 75:438–445

How RA, Dell J, Wellington BD (1986) Comparative ecology of eight species of *Diplodactylus* gecko in Western Australia. Herpetologica 42:471–482

How RA, Dell J, Wellington BD (1990) Reproductive and dietary biology of *Nephrurus* and *Underwoodisaurus* (Gekkonidae) in Western Australia. Rec West Aust Mus 14:449–459

Hutchinson GE (1961) The paradox of the plankton. Am Nat 95:137–145

Jacobs SWL (1984) Spinifex. In: Cogger HG, Cameron EE (eds) Arid Australia. Australian Museum, Sydney, pp 131–142

James CD (1991a) Population dynamics, demography and life history of sympatric scincid lizards (*Ctenotus*) in central Australia. Herpetologica 47:194–210

James CD (1991b) Annual variation in reproductive cycles of scincid lizards (*Ctenotus*) in central Australia. Copeia 1991:742–758

James CD (1994) Spatial and temporal variation in structure of a diverse lizard assemblage in arid Australia. In: Vitt LJ, Pianka ER (eds) Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, NJ, pp 287–333

James CD, Whitford WG (1994) An experimental study of phenotypic plasticity in the clutch size of a lizard. Oikos 70:49–56

Kinghorn JR (1945) The Simpson Desert expedition 1939, scientific reports, no 3. Biology – reptiles and batrachians. Trans Roy Soc South Aust 69:3–9

Losos JB (1987) Postures of the military dragon (*Ctenophorus isolepis*) in relation to substrate temperature. Amphibia-Reptilia 8:419–423

Losos JB (1988) Thermoregulatory correlates of escape behaviour by a desert lizard, *Ctenophorus isolepis*. J Herpetol 22:353–356

Mahon PS (1999) Interactions between rainfall, introduced predators and small mammal populations in the Simpson Desert. PhD thesis, University of Sydney, Sydney

Masters P (1996) The effects of fire-driven succession on reptiles in spinifex grasslands at Uluṟu National Park, Northern Territory. Wildl Res 23:39–48

Mattikallia NM (1996) Time series analysis of historical surface water quality data of the River Glen catchment. J Environ Manage 46:149–172

Meserve PL, Yunger JA, Gutiérrez JR, Contreras LC, Milstead WB, Lang BK, Cramer KL, Herrera S, Lagos VO, Silva SI, Tabilo EL, Torrealba M, Jaksic FM (1995) Heterogeneous responses of small mammals to an El Niño southern oscillation event in northcentral semiarid Chile and the importance of ecological scale. J Mammal 76:580–595

Meserve PL, Gutiérrez JR, Yunger JA, Contreras LC, Jaksic FM (1996) Role of biotic interactions in a small mammal assemblage in semiarid Chile. Ecology 77:133–148

Morton SR (1982) Dasyurid marsupials of the Australian arid zone: an ecological review. In: Archer M (ed) Carnivorous marsupials. Royal Zoological Society of New South Wales, Mosman, pp 117–130

Morton SR, James CD (1988) The diversity and abundance of lizards in arid Australia: a new hypothesis. Am Nat 132:237–256

Murray BR, Dickman CR (1994) Granivory and microhabitat use in Australian desert rodents: are seeds important? Oecologia 99:216–225

Newsome AE, Corbett LK (1975) Outbreaks of rodents in semiarid and arid Australia: causes, preventions, and evolutionary considerations. In: Prakash I, Ghosh PK (eds) Rodents in desert environments. Junk, The Hague, pp 117–153

Orr Y, Shachak M, Steinberger Y (1979) Ecology of the small spotted lizard (*Eremias guttulata*) in the Negev Desert (Israel). J Arid Environ 2:151–161

Pianka ER (1970) On "r" and "K" selection. Am Nat 104:592–597

Pianka ER (1971a) Ecology of the agamid lizard *Amphibolurus isolepis* in Western Australia. Copeia 1971:527–536

Pianka ER (1971b) Comparative ecology of two lizards. Copeia 1971:129–138

Pianka ER (1986) Ecology and natural history of desert lizards. Princeton University Press, Princeton, NJ

Pianka ER (1989) Desert lizard diversity: additional comments and some data. Am Nat 134:344–364

Pianka ER (1994) Biodiversity of Australian desert lizards. In: Peng C-I, Chou CH (eds) Biodiversity and terrestrial ecosystems. Institute of Botany, Academia Sinica, Taipei, pp 259–281

Pianka ER (1996) Long-term changes in lizard assemblages in the Great Victorian Desert: dynamic habitat mosaics in response to wildfires. In: Cody ML, Smallwood JA (eds) Long-term studies of vertebrate communities. Academic Press, New York, pp 191–215

Pough FH (1980) The advantages of ectothermy for tetrapods. Am Nat 115:92–112

Predavec M (1994) Population dynamics and environmental changes during natural irruptions of Australian desert rodents. Wildl Res 21:569–582

Predavec M, Dickman CR (1993) Ecology of desert frogs: a study from southwestern Queensland. In: Lunney D, Ayers D (eds) Herpetology in Australia: a diverse discipline. Royal Zoological Society of New South Wales, Mosman, pp 159–169

Predavec M, Dickman CR (1994) Population dynamics and habitat use of the long-haired rat (*Rattus villosissimus*) in south-western Queensland. Wildl Res 21:1–10

Purdie R (1984) Land systems of the Simpson Desert Region. Natural Resources Series no 2. CSIRO Division of Water and Land Resources, Melbourne

Read JL (1995) Subhabitat variability: a key to the high reptile diversity in chenopod shrublands. Aust J Ecol 20:494–501

Reichman OJ, Prakash I, Roig V (1979) Food selection and consumption. In: Perry RA, Howes KMW (eds) Arid-land ecosystems: structure, functioning and management, vol 1. Cambridge University Press, Cambridge, pp 681–716

Reid A (1995) Factors affecting the local distribution, abundance and species richness of ants in the Simpson Desert. Thesis, University of Sydney, Sydney

Robinson MD (1990) Comments on the reproductive biology of the Namib Desert dune lizard, *Aporosaura anchietae*, during two years of very different rainfall. In Seely MK (ed) Namib ecology: 25 years of Namib research. Transvaal Museum monograph no 7. Transvaal Museum, Pretoria, pp 163–168

Rosenzweig ML (1968) Net primary productivity of terrestrial communities: prediction from climatological data. Am Nat 102:683–718

Saint Girons H (1984) Les cycles sexuels des lézards mâles et leurs rapports avec le climat et les cycles reproducteurs des femelles. Ann Sci Nat Zool Biol Anim Paris 6:221–243

Saint Girons H, Bradshaw SD, Bradshaw FJ (1992) The reproductive cycles of a number of species of lizards from southern and north-western regions of Western Australia. J R Soc West Aust 75:57–64

Schodde R (1982) Origin, adaptation and evolution of birds in arid Australia. In: Barker WR, Greenslade PJM (eds) Evolution of the flora and fauna of arid Australia. Peacock, Frewville, pp 191–224

Smith GT, Leone J, Dickman CR (1997) Small terrestrial vertebrate communities in remnant vegetation in the central wheatbelt of Western Australia. West Aust Nat 21:235–249

Stafford Smith DM, Morton SR (1990) A framework for the ecology of arid Australia. J Arid Environ 18:255–278

Storr GM (1965) The *Amphibolurus maculatus* species-group (Lacertilia, Agamidae) in Western Australia. J R Soc West Aust 48:45–54

Sutherland RA, Bryan RB, Wijendes DO (1991) Analysis of the monthly and annual rainfall climate in a semi-arid environment, Kenya. J Arid Environ 20:257–275

Thompson DB, Brown JH, Spencer WD (1991) Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology 72:852–863

Tinkle DW (1967) The life and demography of the side-blotched lizard, *Uta stansburiana*. Misc Publ Mus Zool Univ Mich 132:1–182

Whitford WG, Creusere FM (1977) Seasonal and yearly fluctuations in Chihuahuan Desert lizard communities. Herpetologica 33:54–65