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Population demography of frillneck lizards (*Chlamydosaurus kingii*, Gray 1825) in the wet-dry tropics of Australia

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Abstract We explore the effects of biotic and abiotic factors on the population demography of frillneck lizards (*Chlamydosaurus kingii*) in the Australian wet-dry tropics. Annual growth rates of males were significantly higher across all body sizes compared to females, resulting in a significant larger maximum body size in males. Both male and female lizards were highly philopatric and 81% of the among-year recapture distances were less than 200 m. Juvenile and adult frillnecks were subjected to low but highly variable annual survival rates. Both proportion of juveniles and relative proportion of reproductive females showed extensive among-year variations. No relationship was, however, observed between proportion of gravid females and that of juveniles captured during the subsequent year. High rainfall in January was negatively correlated with recruitment most likely caused by increased egg/embryo mortality due to flooding of nest sites. We therefore suggest that the lack of association between female reproduction and juvenile recruitment was due to the effects of stochastic variation in January rainfall. Lizard numbers increased during the first five years of the study followed by a decline during the subsequent four years. Our analyses show that annual variation in survival constituted the main determinant in driving the annual change in frillneck numbers. Surprisingly, no relationship was observed between fillneck population dynamics and annual variation in juvenile recruitment. We suggest that the 7-years over which these analyses were conducted were insufficient to detect any significant effects of recruitment on lizard numbers, demonstrating the need for long-term studies to accurately document vertebrate population demographic processes in areas experiencing stochastic variations rainfall such as the Australian wet-dry tropics.

Key words: Australian wet-dry tropics, frillneck lizard, juvenile recruitment, population demography, survival.

INTRODUCTION

Wildlife populations are rarely static in abundance or age structure but the magnitude of variation differs among systems. The factors involved in population demographic processes are therefore clearly of direct relevance to any attempt to manage or conserve wild populations and have hence long been a central focus of wildlife ecology (Lande 1993; Krebs 1996; Gaillard *et al.* 1998).

Assessing the relative impact of such demographic processes on populations in empirical studies is challenging due to the large number of confounding biotic and abiotic variables. In spite of the hurdles, temporal variation in biotic factors such as migration, mortality and reproduction have been demonstrated to have profound effects on the dynamics and demography in numerous animal populations (Gould & Nichols 1998; Hanski 1999; Gaillard & Yoccoz 2003; Madsen *et al.* 2006; Ozgul *et al.* 2006; Proaktor *et al.* 2008; Ujvari *et al.* 2010). In addition, abiotic factors such as climate have long been considered to have a major impact on the population dynamics and demography of Australian biota (Andrewartha & Birch 1954). The Australian climate is dominated by the effects of the El Niño-Southern Oscillation with irregular periodicity and very low predictability. The high stochasticity of the Australian climate engenders a corresponding unpredictable variation in many ecological systems and has spawned a long-standing scepticism by Australian ecologists towards equilibrial models which emphasize biotic rather than abiotic factors as a the major process involved in population dynamics and demography (Andrewartha & Birch 1954; Braithwaite 1990; White 1993; Flannery 1994; Madsen & Shine 1999a,b; Madsen *et al.* 2006; Ujvari *et al.* 2010, 2011a,b).

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In the present study we describe and interpret biotic and abiotic factors, affecting the population demography of a large and arboreal squamate reptile, the frillneck lizard (*Chlamydosaurus kingii*), which has been the subject of our detailed studies in the wet-dry tropics of Australia since 2003.

MATERIALS AND METHODS

Study area and species

The study was conducted at Fogg Dam Conservation Reserve situated approximately 60 km south-east of Darwin in the Top End of the Northern Territory of Australia. The Savannah woodland of the study area is dominated by woollybutts (*Eucalyptus miniata*, Shauer 1843) with an understorey consisting of sparse low growing grasses and herbs.

The study area lies within the 'wet-dry' tropics of Australia where temperatures are high year-round (mean daily maximum air temperature > 30°C in every month) but precipitation is highly seasonal. More than 75% of the 1533 mm mean annual rain falls during a brief four month 'wet-season', from December to March, and only a small fraction of the precipitation falling during the 5 month dry season. Climatic data were obtained from Lambell's Lagoon meteorological station situated approximately 5 km north-west of the study area.

Frillneck lizards inhabit tropical Savannah woodlands throughout the northern part of Australia and southern New Guinea (Cogger 2002). This large arboreal lizard is highly sexually size dimorphic, and in our study area the body mass of the largest female and male captured was 389 and 719 g respectively. Male frillnecks are territorial and the frill is displayed in male-male interactions during the mating season (Shine 1990). During the dry season, the lizards are virtually inactive, and remain perched in high trees (Christian & Green 1994). Field work was therefore undertaken when rain and thunderstorms had caused an increase in humidity and concomitant increase in lizard activity, that is, from late September to the mid December in 2003, 2005 and annually from 2007 to 2013.

Lizards were located from a slow-moving car, along a 10 km dirt track within the reserve and captured by hand or by noosing using a telescopic rod. The car odometer was used to determine the capture location of each lizard with an accuracy of 50 m. All lizards were released at the exact place of capture within 15 min. Snout–vent length (SVL) and mass were recorded to the nearest millimetre and gram of each captured lizard. The lizards were sexed by cloacal probing, and were permanently marked by branding symbols on the lateral surface of the anterior part of the tail (for further details see Madsen & Shine 2000). A total of 728 lizards were captured (373 females and 355 males) during the 9-year study. To quantify among-year variation in lizard body mass we calculated residual body mass (henceforth RBM) from a general linear regression of ln-transformed mass on ln-SVL. Gravid females were excluded from the RBM calculations.

Frillneck reproduction in the Top End of Australia is highly seasonal with the majority (85%) of gravid females being encountered from November to January (Griffiths 1999). The smallest reproductive female encountered in the present study had a SVL of 168 mm and our annual estimates of reproductive females were therefore based on females captured in November and December with an SVL equal to or more than 168 mm. The SVL of juveniles (<1 year old) did not overlap with that of older lizards (SVL: 78–149 mm *vs*. 160–280 mm), the assignment to this cohort could therefore confidently be based on their SVL.

Statistical analyses

Analyses were carried out using JMP version 5.1 (SAS Institute 1998). As comparison of traits such as SVL and RBM included lizards marked during previous years, the random effects option available in JMP was used in all analyses. We used the Jolly–Seber open population model available in the software package POPAN-5 to estimate the numbers of frillneck lizards each year. The program provides a parameterization of the Jolly–Seber model that is particularly robust (Schwarz & Arnason 1996) and computes survival rates and population size (with associated standard errors) based on a demographic model independently proposed by Jolly (1965) and Seber (1965).

RESULTS

Annual growth rates of male frillneck lizards were faster than those of females across all body sizes (ANCOVA with sex as factor, SVL as covariate and annual growth as dependent variable: $F_{2,121} = 550.6$, $P < 0.0001$, sex: $F_1 = 496.0$, $P < 0.0001$; SVL: $F_1 = 496.0$, $P < 0.0001$; slope: $F_1 = 0.002$, $P = 0.89$; Fig. 1), resulting in a larger body size in males compared to females (ANOVA based on all lizards captured; $F_{1,959} = 222.8$, $P < 0.0001$; mean SVL: 222.7 and 190.5 mm, respectively).

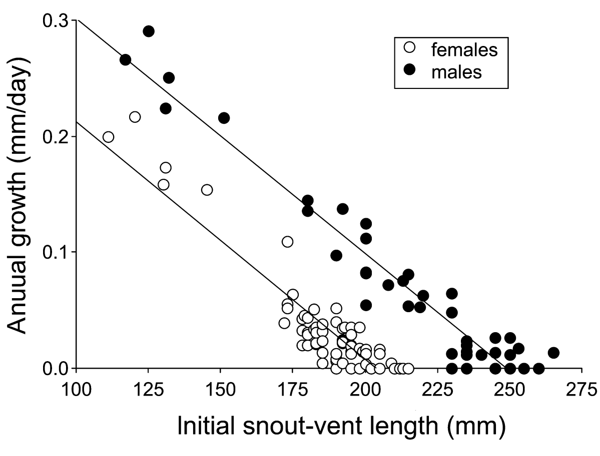

Fig. 1. Annual growth rates and initial snout–vent length of male ($n = 48$) and female ($n = 76$) frillneck lizards.

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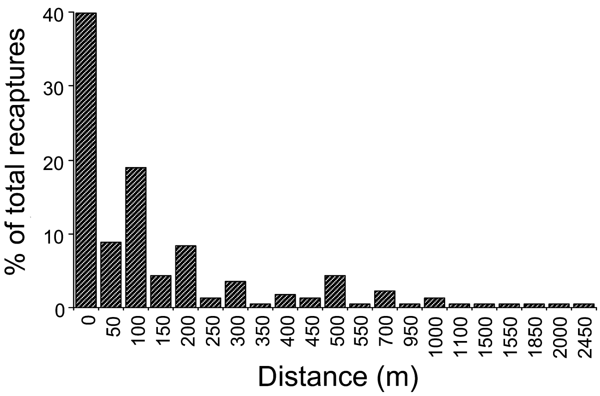

Fig. 2. Proportion of among-year recapture distances of all the 228 frillneck lizards. Note that the scale on the *x*-axis is not linear.

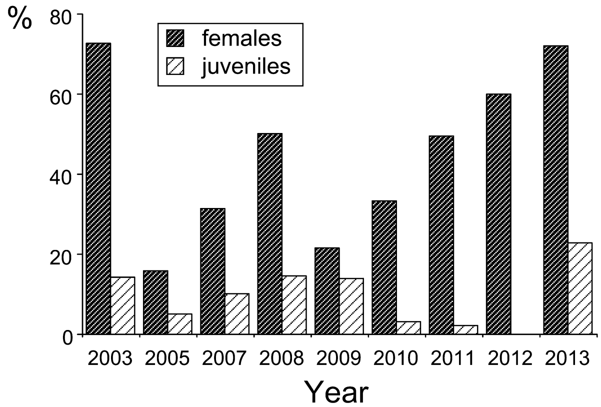

Fig. 3. Annual proportion of gravid female and proportion of juvenile frillneck lizards. Annual proportions of gravid females calculated from total numbers of adult females captured annually and annual proportion of juveniles calculated from the total numbers of all lizards captured annually.

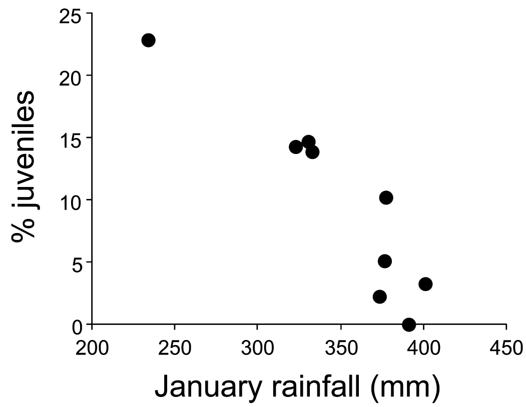

Fig. 4. Relationship between annual proportion of juveniles and mean annual rainfall in January. Annual proportion of juveniles calculated from the total numbers of all lizards captured annually.

The among-year recaptures demonstrated that both male and female lizards were highly philopatric (Fig. 2); 90 of the 228 recapture lizards (39.5%) were found at less than 50 m from their locations during previous years, and 184 were recaptured less than 200 m from their initial capture site (81%; Fig. 2). Moreover, we did not observe any among-year variation in annual recapture distances (Kruskal-Wallis test: $\chi^2 = 4.55$, $P = 0.72$, d.f. = 7). However, mean among-year recapture distances in males were significantly higher than those recorded among female lizards (Mann–Whitney *U*-test: Z = 4.51, $P < 0.0001$; mean male recapture distance 264 m, SE =39.2, mean female recapture distance 123 m, SE = 24.9).

Between 2007 and 2013 there was a substantial among-year variation in frillneck lizard survival rates (ranging from 25.2% to 55.0%; mean: 41.0%), but no significant difference in male and female survival ($t_{10} = 0.11$, $P = 0.91$).

We also observed a substantial among-year variation in the proportion of gravid females, ranging between 15.8% and 72.7% (mean: 45.2%; Fig. 3). The annual proportion of gravid females showed a significant positive relationship with mean annual RBM (Spearman rank correlation: $R = 0.70$, $P = 0.036$, $n = 9$, note that no gravid females were used in the RBM calculations). However, temporal variation in wet-season rainfall was not correlated with lizard mean annual RBM (Spearman rank correlation: $R = 0.07$, $P = 0.86$, $n = 9$). Moreover, lizard RBM did not affect their recapture probability (logistic regression: $\chi^2 = 0.04$, $P = 0.84$, d.f. = 1).

The annual proportion of juveniles among all lizards captured ranged from 0 to 22.9% (mean: 9.6%; Fig. 3), but we did not observe any association between the annual proportion of gravid females and the proportion of juveniles captured during the subsequent year (Spearman rank correlation: $R = 0.31$, $P = 0.54$, $n = 6$). No relationship between mean annual wet-season rainfall and proportion of juveniles was observed (Spearman rank correlation: $R = -0.43$, $P = 0.24$, $n = 9$) but there was a highly significant negative relationship with mean January rainfall (Spearman rank correlation: $R = -0.83$, $P = 0.005$, $n = 9$; Fig. 4), thus significantly higher proportions of juveniles were observed in years with lower January rainfall.

The population estimates showed that during the first five years of our study frillneck number increased from 162 in 2003 to an estimated 289 lizards in 2009 followed by a decline in numbers during subsequent four years and in 2013 the population was estimated to consist of 112 lizards (Fig. 5). In order to investigate factors that may have affected the frillneck lizard population dynamics we calculated the annual changes in population size from 2007 to 2013 (i.e. the ratio of population sizes in $\text{year}_{n+1}/\text{year}_n$). We observed a

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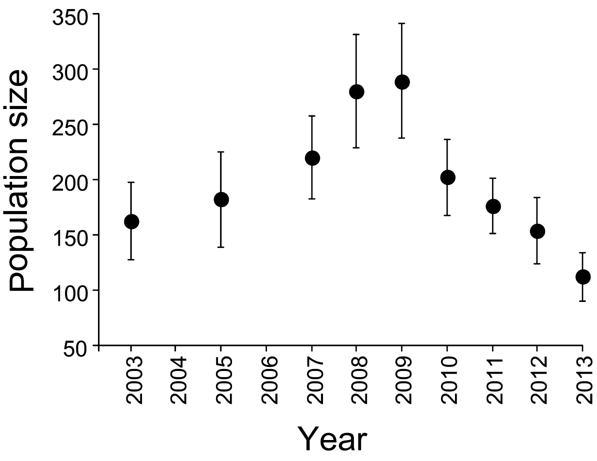

Fig. 5. Annual estimated frillneck lizard population size with associated SE based on the results from the Jolly-Seber open population model available in Popan-5.

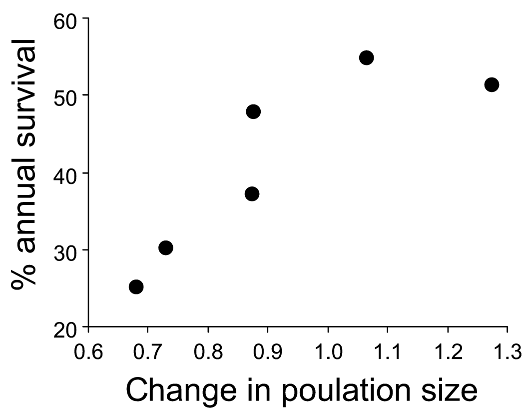

Fig. 6. Relationship between annual survival rates and annual change in frillneck population size.

significant positive correlation between the change in population numbers and annual mortality rates (Spearman rank correlation: $R = 0.94$, $P = 0.005$, $n = 6$; Fig. 6) but no correlation between the former variable and recruitment (i.e. the proportion of juveniles in year$_n$) was observed (Spearman rank correlation: $R = 0.09$, $P = 0.87$, $n = 6$).

DISCUSSION

In many lizards male mating success is strongly enhanced by larger body size (e.g. in lizards; Lebas 2001; Wikelski & Romero 2003; Salvador *et al.* 2008). We therefore suggest that the faster growth rates and larger body size in males compared to female frillneck lizards is driven by sexual selection to enhance male reproductive success. Griffiths (1999) found that male frillneck home ranges were significantly larger than that of females. The larger male mean annual recapture distances than those of females most likely reflect the difference in home range size between the two sexes. As suggested by Griffiths (1999) the larger male home ranges observed in the present study will enable access to a greater number of females and may therefore result in a concurrent increase in male fitness.

In spite of the large body size of both male and female frillnecks, our results show that the lizards suffered from surprisingly low annual survival rates. In other organisms living in the wet-dry tropics such as water pythons (*Liasis fuscus*) the survival/recapture rate were positively correlated with the RBM scores (Madsen *et al.* 2006). However, in our frillneck population no such relationship was observed strongly suggesting that RBM did not affect annual survival rate. This begs the question what could be the cause of the low and highly variable annual survival rate among both male and female the frillneck lizards?

Abiotic factors such as late dry-season hot bush fires may result in substantial reduction in frillneck lizard numbers in the Savannah woodlands of the Top End of the Northern Territory (Griffiths & Christian 1996a; Ujvari *et al.* 2008). However, the study area was only subject to 'cold' dry season bush fires which during the 9-year study did not cause any visible damage to the area. Therefore it is highly unlikely that the large among-year variation in lizard survival was caused by concomitant variation in fire regimes.

Biotic factors such as predation contribute to temporal variation in survival rates in numerous vertebrate populations (Donovan & Thompson 2001; Gaillard & Yoccoz 2003; Valkama *et al.* 2005; Miller *et al.* 2006; Ellis *et al.* 2007; Lingle *et al.* 2008; Johnson & Zúñiga-Vega 2009). Several snake species occur in our study area, but only large species such as pythons are able to feed on adult frillneck lizards. Such events, however, appear to be extremely rare as during a > 20 year study of water pythons (*Liasis fuscus*) only one frillneck lizard was recorded as a prey item (Ujvari *et al.* 2011a). Two large varanids, sand goannas (*Varanus gouldi*) and yellow-spotted goannas (*V. panoptes*) were occasionally observed within the study area but since 2007 they have disappeared due to poisoning by invading cane toads (Ujvari & Madsen 2009). It is therefore highly unlikely that the temporal variation in frillneck survival has been caused by snake or varanid predation. Moreover, frillneck lizards in our study area do not feed on cane toads (Ujvari *et al.* 2011c) and the variation in survival is certainly not caused by the lizards succumbing to cane toad toxins. On few occasions we have observed dingoes (*Canis lupus dingo*) in the study area. However, the diet of this canine rarely consists of reptiles (Brook & Kutt 2011), and it is therefore unlikely that dingo predation has contributed to the frillnecks highly variable among-year survival rates.

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Several Australian raptors frequently include reptiles in their diet (Aumann 2001) and during the 9-year study four species of raptors have been observed in the study area; brown falcon (*Falco berigora*), collared sparrowhawk (*Accipiter cirrhocephalus*), brown goshawk (*A. facsiatus*) and whistling kite (*Haliastur sphenurus*) of which the latter three were observed almost daily. Except for the collared sparrowhawk the diets of the other three raptors frequently include squamate reptiles and in south-western part of the Northern Territory 80% of the diet of brown goshawks consisted of lizards, mainly agamids (Aumann 2001) and we therefore strongly suspect raptors such as brown goshawks may constitute a major source of predation on adult frillneck lizards in our study area. Future field work is, however, clearly needed in order to robustly determine the cause of both the temporal variation and the low annual survival of this iconic lizard.

Most squamate reptiles rely on stored energy to support reproductive expenditure and the decision to reproduce in a given year depends upon the magnitude of the reserves (Naulleau & Bonnet 1996; Madsen & Shine 1999b). In the wet-dry tropics of Australia, temporal variation in squamate residual body mass (RBM) has been linked to annual variation in prey abundance (Madsen *et al.* 2006; Ujvari *et al.* 2010, 2011a). Moreover, several studies have shown that temporal fluctuations of gravid females are caused by concomitant variations in prey abundance (Wise 1979; Madsen *et al.* 2006; Brown & Shine 2007). The significant positive relationship between temporal variation in frillneck RBM and proportion of gravid females may therefore be caused by a concomitant temporal variation in prey abundance. Surprisingly for such a large lizard the main prey of frillnecks consists of termites (Griffiths & Christian 1996b). To our knowledge, however, no long-term termite population studies have been conducted (Lepage & Darlington 2000), and hence we do not have access to data supporting (or contradicting) that the temporal variation in RBM and proportion of gravid female frillnecks was caused by temporal variation in termite numbers.

In contrast to other studies (Sillett *et al.* 2000; Møller 2002; Madsen *et al.* 2006) we did not observe any association between temporal variation in female reproductive output and subsequent juvenile recruitment. The combination of highly seasonal reproduction (Griffiths 1999) and a 2- to 3-month incubation period (Harlow & Shine 1999) results in the vast majority of frillneck eggs being located in nest burrows in January. Like other oviparous reptiles, the incubation period of frillneck eggs is temperature-dependent, ranging from 124 days at 26°C to 71 days at 33°C (Harlow & Shine 1999). The combination of reproductive seasonality and a 2- to 3-month incubation period results in the vast majority of frillneck eggs being located in nest burrows in January. The microclimate, such as, soil moisture, in such burrows has a significant effect on embryo survival as well as offspring phenotypes in numerous oviparous reptiles (Elphick & Shine 1998; Hokit & Branch 2004; Reedy *et al.* 2013). A dramatic example of how soil moisture may affect embryo survival was recorded approximately 100 km west of our study area in January 2009 when a torrential downpour flooded several frillneck nest sites resulting in the death of all the eggs/embryos (P. Fisher, unpublished, 2009). This observation is unlikely to have been an exceptional incidence as such rain-induced egg/embryo mortality has been observed in loggerhead turtles (*Caretta caretta*) (Kraemer & Bell 1980), saltwater crocodiles (*Crocodylus porosus*) (Magnusson 1982), and in birds such as least terns (*Sterna antillarum*) and piping plovers (*Charadrius melodus*; Sidle *et al.* 1992). We consequently suggest that the lack of relationship between female reproductive output and juvenile recruitment was caused by excessive January rainfall leading to lower frillneck egg/embryo survival and hence lower juvenile recruitment.

During the first five years of our study estimated frillneck number increased from 162 in 2003 to 289 lizards in 2009 where after numbers declined, and in 2013 the population was estimated to consist of 112 lizards. As our analyses of frillneck spatial distribution showed that the vast majority of the lizards were highly philopatric and that the among-year level philopatry did not change during the study it is unlikely that the among-year variation in frillneck numbers was caused by concomitant temporal variation in migration.

In a study of water pythons in the same general area Madsen *et al.* (2006) found that recruitment, annual survival and prey abundance all had significant and independent effects on population dynamics (i.e. the ratio of population sizes in $\text{year}_{n+1}/\text{year}_{n}$). In the present study however, the only factor that affected frillneck lizard population dynamics was the temporal variation in survival, hence strongly suggesting that annual variation in predation was the main factor affecting the annual variation in frillneck lizard numbers.

In other organisms living in the wet-dry tropics of Australia such as dusky rats (*Rattus collettii*), water pythons (*Liasis fuscus*) and Arafura filesnakes (*Acrochordus arafurae*) abiotic factors such as stochastic variation in rainfall patterns have been shown to massively influence population demographic processes such as survival and recruitment (Madsen & Shine 1999a; Madsen *et al.* 2006; Ujvari *et al.* 2010, 2011a,b). The negative correlation between January rainfall and juvenile recruitment (i.e. excessive rainfall resulting in high egg/embryo mortality) suggests that abiotic factors such as rainfall do have an impact on frillneck lizard recruitment.

The lack of a correlation between recruitment (i.e. the proportion of juveniles) and frillneck lizard

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numbers is, however, puzzling, as temporal variation in recruitment would be expected to affect population dynamic processes. Although our analyses of the effect of annual recruitment on among-year variation in frillneck numbers were conducted over 7 years (2007 to 2013), we suspect that this may have been a too short time period to detect any significant effect of recruitment on the population dynamics. This is supported by our long-term research (>20 years) on water pythons, where reaction norms recorded over 16 years of 'normal' (albeit highly variable) climatic conditions gave little insight into the population's response to a more extreme nutritional crisis (Ujvari *et al.* 2011c). The apparent lack of a relationship between recruitment and frillneck lizard population dynamics observed in the present study further confirms the need for long-term studies to accurately document vertebrate population demographic processes in areas experiencing stochastic variations in climatic conditions such as the Australian wet-dry tropics.

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