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Floods and famine: climate-induced collapse of a tropical predator-prey community

Beata Ujvari[1], Gregory Brown[2], Richard Shine[2] and Thomas Madsen*[,3,4]

[1]*Centre for Integrative Ecology, School of Life & Environmental Sciences, Deakin University, Geelong, Vic., Australia;* [2]*School of Biological Sciences, University of Sydney, Sydney, NSW 2006, Australia;* [3]*School of Molecular Biosciences, University of Sydney, Sydney, NSW 2006, Australia; and* [4]*School of Biological Sciences, University of Wollongong, Wollongong, NSW 2522, Australia*

Summary

1. Will climate change threaten wildlife populations by gradual shifts in mean conditions, or by increased frequency of extreme weather events?

2. Based on long-term data (from 1991 to 2014), the aim of the present study was to analyse and compare the sensitivity of predator–prey demography to extreme climatic events versus normal, albeit highly variable, annual deviations in climatic conditions in the Australian wet–dry tropics.

3. From 1991 to 2005, predators (water pythons, *Liasis fuscus*) and their main prey (dusky rats, *Rattus colletti*) showed significant climate-driven fluctuations in numbers.

4. These fluctuations were, however, trivial compared to the impact of two massive but brief deluges in 2007 and 2011, which virtually eliminated the dusky rats. The two floods resulted in the pythons experiencing an unprecedented famine in seven out of the last 8 years causing a massive shift in python demography, that is a significant reduction in feeding rates, reproductive output, growth rates, relative body mass, survival, mean body length and numbers (from 3173 in 1992 to 96 in 2013).

5. Our results demonstrate that attempts to predict faunal responses to climate change, even if based on long-term studies, may be doomed to failure. Consequently, biologists may need to confront the uncomfortable truth that increased frequency of brief unpredictable bouts of extreme weather can influence populations far more than gradual deviations in mean climatic conditions.

Key-words: Australia, extreme climatic events, predator–prey population demography, rodent, squamate reptile, wet–dry tropics

Introduction

The world's climate is changing, in complex ways (Parmesan 2006; Mora *et al.* 2013; Garcia *et al.* 2014). To understand how these changes affect wildlife populations, we need to identify mechanisms of impact. One fundamental distinction is between gradual shifts in average weather conditions, versus an increased frequency of extreme climatic events, because plausibly, animal populations could be affected by changes in either of these two parameters. If an increased frequency of extremes is biologically more important than shifting averages, managers need to allocate more effort towards ameliorating 'extreme' effects. Climatic models and recent empirical data strongly suggest that extreme climatic events will become more common during future years (Easterling *et al.* 2000; Parmesan, Root & Willig 2000; Diffenbaugh *et al.* 2005; Kerr 2011; Schiermeier 2011; Coumou & Rahmstorf 2012).

Studies conducted in temperate regions have shown that extreme climatic events may cause significant shifts in the demography of vertebrate populations (Tompa 1971; Garel *et al.* 2004; Altwegg *et al.* 2006; Wilson & Peach 2006; Frederiksen *et al.* 2008). For example, Thibault & Brown (2008) showed that an extreme flood in a Chihuahuan desert rodent community caused major dramatic changes in the relative abundance of different taxa such that previously dominant species became rare, and pre-existing ecological interactions underwent wholesale reorganization. However, to our knowledge, no long-term field data exist to compare the impacts of gradual shifts in

*Correspondence author. E-mail: madsen@uow.edu.au

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mean, albeit highly variable, climatic conditions *versus* faunal responses to increased frequency of extreme climatic conditions in tropical ecosystems.

Since 1991, we have studied the population demography of a large tropical predator, the water python (*Liasis fuscus*) and its main prey the dusky rat (*Rattus colletti*) on the Adelaide River floodplain in the Australian wet–dry tropics. Over the first 16 years of our work, annual variation in rainfall caused rat numbers to vary over a sixfold range, generating up to twofold changes in python abundance (Madsen *et al.* 2006a). We have previously reported how a brief extreme flood in March 2007 affected female python traits such as body length and reproduction (Ujvari *et al.* 2011a). However, since the publication of this study, another deluge, caused by cyclone Carlos, resulted in another massive brief flooding event in February 2011, similar to the flood recorded in 2007. The two floods resulted in a virtual elimination of dusky rats (due to drowning) during 7 of the last 8 years and, consequently, affected predator demographic traits such as python feeding rates, reproductive output, growth rate, survival, body size and ultimately numbers more dramatically than we had documented over the preceding 16 years of our study. The results from the present study suggest that that increased frequency of extreme climatic events will result in dramatic shifts in a tropical predator–prey community, exceeding the effects of gradual deviations in mean climatic conditions.

Materials and methods

STUDY AREA AND SPECIES

Our study area is situated *c.* 60 km south-east of Darwin in the Northern Territory of Australia, within the 'wet–dry' tropics (131°18′48·19″E, 12°34′14·81″S). 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 1440 mm mean annual rainfall occurs during the brief wet season, December to March (data from Middle Point meteorological station, situated *c.* 2 km from our study area. The Adelaide River floodplain is a flat, treeless area formed by silt deposition formed by the Adelaide River, and the vegetation consists primarily of native sedges and grasses.

Water pythons are large (to 3 m) non-venomous snakes widely distributed across tropical Australia (Cogger 2000). Results in the present study are based on capture–mark–recapture study of 5739 individually marked pythons captured from 1991 to 2014 at Fogg Dam Conservation Reserve. Because water pythons are primarily nocturnal, the snakes were captured over a two-hour period each night beginning *c.* 30 min after sunset. Snakes were located by spotlighting (from a slowly moving vehicle) along the 1·3-km-long Fogg Dam wall. From 1991 to 1994, fieldwork was conducted for 6 months (August to December) and from 1995 to 2003 during 2 months (August to September). No fieldwork was conducted in 2004 or 2006, and in 2005, the fieldwork was from late October to December. Similar to the 9-year period from 1995 to 2003, between 2007 and 2014 field work again was conducted for 2 months during August and September.

All pythons were individually marked by ventral scale clipping, and we recorded body length, mass and female reproductive status. The reproductive cycle of the pythons in our study area is highly synchronous, and gravid females are easily recognizable by body shape during August–October (Madsen *et al.* 2006a). Consequently, we do not have data on female reproduction in 2005 (see above). Prey records were obtained by palpation and by faecal analyses. All snakes were released at their site of capture within 24 h. Annual python growth rates were quantified as residuals from a general linear regression of annual growth increment (in mm/day) on python body length. Python relative body mass (RBM) was calculated as residual scores from a general linear regression of ln-transformed mass on ln body length.

In our study area, water pythons feed primarily on a single species of small (up to 210 g) native rodent, the dusky rat (*Rattus colletti*; Madsen *et al.* 2006a). Data on the demography of dusky rats were derived from annual 5-day trapping periods on the Adelaide River floodplain in August. We deployed 50 Elliott traps, baited with rolled-oats, at 10-m intervals along a 500-m transect, and the traps were placed at the same positions each year. All rats were given an individually numbered ear tag to ensure that our counts of rat numbers did not include repeated captures of the same individual.

STATISTICAL ANALYSES

We used JMP 5.1 (SAS Inst., Cary, NC, USA) for statistical analyses. Animal identification was employed as a random effect in analyses including recaptured snakes (i.e. among-year variation in proportions of snakes with prey, proportions of gravid females, growth rates, RBM and mean body length). The program MARK (White & Burnham 1999) was used to compare the fit of 12 mark–recapture models (Table 1). Constraints on the recapture (p) and survival (phi) parameters varied among the different models as follows:

1. (.) a single constant survival rate across all years of the study
2. (t) time-dependent survival rate (phi(t)), differing among years.
3. (rat#) rat-dependent covariate, modelled as a linear continuous, effect of # of rats trapped in each year. It assesses the prediction that python demography changes in a linear manner with rat abundance.
4. (hi-lo) binomial covariate of numbers of rats trapped; high abundance years (> 10 rats trapped) vs. low abundance years (< 10 rats trapped). This alternative means of modelling rat numbers may better capture threshold effects of prey numbers, for example, if maximal survival occurs at less than maximal rat density. It assesses the prediction that rates of python survival or recapture differ between periods of high vs low rat density.
5. (pre–post) binomial covariate of time relative to the 2007 flood event; pre-flood (1991–2005) and post-flood (2007–2014). This reconfigures temporal effects to model changes in parameter estimates coincident with the flooding event. It assesses the prediction that rates of python survival or recapture were affected by the flood (differ between pre-flood and post-flood periods).

We used 100 bootstrap simulations to assess goodness-of-fit of the fully time-dependent model. We divided the observed deviance of this model by its degrees of freedom and then divided the resultant value (= $\hat{c}$) by the average $\hat{c}$ of the 100 bootstrap simulations. The ratio of observed to average $\hat{c}$'s (=1·24) indicated modest overdispersion, and we adjusted models accordingly. Model fit was assessed using quasi AICc values. In addition, we calculated a pseudo-R^2 value for each covariate model to describe the proportion of deviance (dev) it explained relative to constant- and time-dependent models (e.g. Le Bohec *et al.* 2008). The pseudo-R2 was calculated according to Burnham & Anderson (2002) as:

$$[\text{dev(constant)} - \text{dev(covarite)}]/[\text{dev(constant)} - \text{dev(time-dependent)}]$$

We used the implementation of POPAN (Schwarz & Arnason 1996) in the MARK program (White & Burnham 1999) to estimate water python population numbers over the study. We assessed

Table 1. Rankings of the 12 Cormack–Jolly–Seber (CJS) models of water python survival (phi) and recapture probability (*P*).

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Para.	QDeviance	Pseudo-R^2
Phi(pre–post) p(*t*)	13 145·71	0·00	0·89	1·00	23	1504·55	0·96
Phi(hi-lo) p(*t*)	13 150·20	4·49	0·09	0·11	23	1509·04	0·96
Phi(t) p(*t*)	13 153·28	7·57	0·02	0·02	41	1475·79	1·00
Phi(rat) p(*t*)	13 201·00	55·29	0·00	0·00	23	1559·84	0·90
Phi(.) p(*t*)	13 246·88	101·17	0·00	0·00	22	1607·73	
Phi(t) p(pre–post)	13 377·35	231·64	0·00	0·00	21	1740·22	0·68
Phi(*t*) p(.)	13 411·09	265·38	0·00	0·00	22	1771·94	
Phi(pre–post) p(pre–post)	13 615·31	469·60	0·00	0·00	4	2012·30	0·34
Phi(hi-lo) p(hi-lo)	13 655·74	510·03	0·00	0·00	4	2052·72	0·29
Phi(pre–post) p(.)	13 656·64	510·93	0·00	0·00	3	2055·63	0·29
Phi(rat) p(rat)	13 706·79	561·08	0·00	0·00	4	2103·77	0·23
Phi(.) p(.)	13 891·43	745·72	0·00	0·00	2	2292·42	0·00

four POPAN models in which phi and p were either time-dependent or constant, and where the entry probability parameter (pent) was time-dependent. We took abundance estimates from the best-fitting model, which was {phi(*t*) p(*t*) pent(*t*)}.

Results

Monsoonal rainfall inundates the Adelaide River floodplain every wet season, causing a gradual increase in water levels. On 3 March 2007, however, 244 mm of rain fell in the Adelaide River catchment (the highest daily rainfall recorded at Adelaide River meteorological station since records began in 1956), *c*. 100 km upstream (south) from our study site. The subsequent 'inland tsunami', a tidal wave about 1 m high, inundated the entire Adelaide River floodplain within a few hours. Four years later (15–17 February 2011), tropical cyclone 'Carlos' produced a deluge of 308 mm of rainfall at Fogg dam [the highest rainfall recorded in Middle Point meteorological station (2 km from Fogg Dam) since records began in 1957] which, similar to the flood recorded in March 2007, rapidly flooded the Adelaide River floodplain.

Prior to the first flood in 2007, the number of dusky rats captured on our trapping transect ranged from 24 (in 1994) to 138 (in 1991). However, the inland tsunami of 2007 drowned virtually all the rats (Fig. 1a). Rat numbers recovered in 2010, but it was short-lived. In 2011, cyclone Carlos caused another mass drowning and near-eradication of the dusky rat population (Fig. 1a).

These crashes in rodent abundance had dramatic consequences for their main predators, the water pythons. The proportion of pythons containing freshly ingested prey fell sharply (Fig. 1b). The restriction in food intake prevented female pythons from reproducing, no gravid females were recorded in 2008, 2009, 2012 or 2013 and only one gravid female was captured in 2014 (Fig. 1c). Although annual residual growth rates of pythons varied significantly during the study ($F_{18,956} = 18{\cdot}3$; $P < 0{\cdot}0001$; Fig. 1d), a post hoc test showed that annual growth rates from 2007 to 2012 were significantly lower than in any other year of our study (Fig. 1d). We also observed significant annual variation in python relative body mass ($F_{21,\ 6479} = 96{\cdot}3$, $P < 0{\cdot}0001$) and a post hoc test revealed that after the floods had drowned their prey, pythons became increasingly emaciated and relative body mass was significantly lower in 2008, 2009, 2013 and 2014 than during the other years of the study (Fig. 1e).

The top five mark–recapture models all had time-dependent recapture probabilities. Not surprisingly, the best-fitting model was when survival was constrained to take on different values for the pre- and post-flood periods. This model had approximately four times more support than the second-ranked model (Table 1). Prior to the 2007 and 2011 floods, water python survival rate was 0·799 (95% CI = 0·787–0·809), but dropped to 0·449 (95% CI = 0·402–0·497) after the two floods (Fig. 1f, Table 1). The second-ranked model was one that allowed survival rate to take on one value during periods with high (>10) rat numbers (1991–2005, 2010, 2011), and another value during periods with low (<10) rat numbers (2007–2009, 2012–2014). This model estimated python survival during high rat years to be 0·799 (95% CI = 0·788–0·810) and 0·430 (95% CI = 0·382–0·481) during low rat years (Table 1).

Although python annual mean body lengths varied significantly during the study ($F_{21,8104} = 20{\cdot}0$, $P < 0{\cdot}0001$), a post hoc test showed that mean body length was significantly lower from 2008 to 2014 compared to previous years (Fig. 1g). Our data strongly suggest that the reduction in body length was caused by a combination of higher mortality of large pythons and significantly reduced growth rates of the surviving smaller snakes. The low survival rates after the first flood combined with an absence of recruitment (due to cessation of breeding) resulted in a massive decline in water python numbers (Fig. 1h) from 3173 in 1992 to 96 in 2013.

Further evidence for the causal link between rat abundance and python demography comes from strong relationships between annual variation in rat numbers and python feeding rates, proportions of gravid females, residual growth rates, relative body mass, annual survival rates, mean body length and python numbers ($r^2 = 0{\cdot}91$, $P < 0{\cdot}0001$, $n = 22$; $r^2 = 0{\cdot}79$, $P < 0{\cdot}0001$, $n = 21$; $r^2 = 0{\cdot}58$, $P < 0{\cdot}0001$, $n = 19$; $r^2 = 0{\cdot}73$, $P < 0{\cdot}0001$,

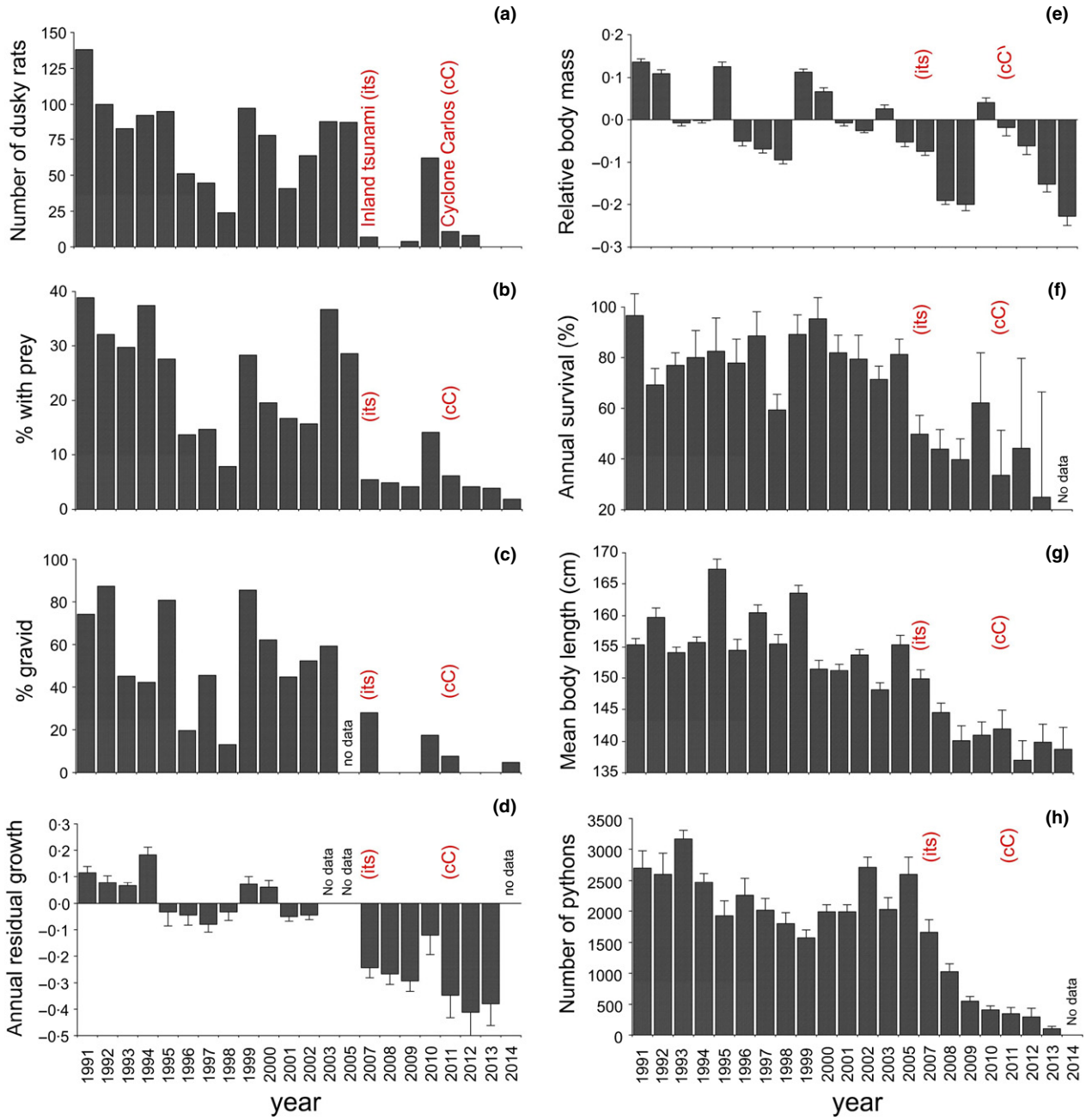

Fig. 1. Population demography of dusky rats and water pythons. Annual variation in rat numbers (a), python feeding rate (b), proportion of gravid female pythons (c), residual growth rate (d), relative body mass (e), annual survival (f), mean body length (g) and python numbers (h). Vertical bars in panel (d–h) depict associated SE. As no field work was conducted during the python's reproductive season in 2005, no data are available for this year in panel c. The estimates of residual growth rate (panel d) require data collected during consecutive years; hence, no data are available for 2003 and 2005. The Jolly–Seber model did not provide data for annual survival in 2014 (panel f) and python numbers in 2014 (panel h).

$n = 22$; $r^2 = 0{\cdot}68$, $P < 0{\cdot}0001$, $n = 21$; $r^2 = 0{\cdot}50$, $P = 0{\cdot}0002$, $n = 22$; $r^2 = 0{\cdot}51$, $P = 0{\cdot}0003$, $n = 21$, respectively: all significant after sequential Bonferroni corrections).

Discussion

Our data provide a strong cautionary note for ecologists and wildlife managers who seek to predict the effects of climate change. The water pythons and dusky rats of the Adelaide River floodplain have been studied in more detail, for longer, than most tropical predator–prey communities. We thought that we understood the factors that drive annual variation in python demography, but we were wrong. Two brief extreme weather events were game-changers, in terms of their effects on the population demography of the predator–prey community. Because we monitored this system for 16 years prior to the two deluges

that caused the rapid inundation of the floodplain (the only times we have ever seen this happen), the inference of causation – that the subsequent massive reduction in rat and python numbers was a direct result of the flooding in 2007 and 2011 – is strong. As a direct result of the two floods, water pythons have faced an unprecedented famine in seven out of the last 8 years. Our previous studies demonstrate that the dramatic reduction in water python number from the study site was not due to emigration (Ujvari, Shine & Madsen 2011b). The present study shows that the decrease in python numbers was caused by a combination of increased mortality and a virtual lack of recruitment.

Other studies have demonstrated that climate-induced prey shortages may affect the mortality rates of some age and/or body sizes of predators more than others (Bumpus 1899; Brown & Brown 1998; Grant & Grant 2002; Wikelski 2005; Ujvari *et al.* 2010). The results from the present study show that for larger pythons (with higher maintenance costs), the virtual elimination of their main food supply caused a massive increase in mortality between 2007 and 2008 and from 2008 to 2009, with a concomitant reduction in overall python body sizes. After the two floods, the surviving pythons were mainly small slow-growing snakes that shifted their diet from dusky rats to alternative, less abundant, prey such as lizards and snakes (Ujvari, Shine & Madsen 2011b). Similar significant climate-induced shifts in body size in other study systems can be caused by a range of ecological factors (Sheridan & Bickford 2011), but our study identifies nutrient limitation as the main cause for the dramatic reduction in python body size.

Virtually, all rats on the floodplain were drowned by the two massive deluges in 2007 and 2011. Although unique during the present study, earlier research on dusky rats on the Adelaide River floodplain reported a similar phenomenon: a cyclonic deluge on 24 December 1974, resulted in rapid and massive flooding, causing dusky rats numbers to plummet from high levels in 1972 through 1974 to zero in 1975; only three rats were trapped in 1976 (Redhead 1979). Similar to the present study, Redhead (1979) attributed this virtual disappearance of rats to drowning. We have no data on how the dramatic reduction in rat numbers in 1975 and 1976 affected the demography of the water pythons, but both rat and water python numbers had recovered by the time the present study was initiated in 1991. Thus, for 31 years (1974 to 2006), the Adelaide River floodplain did not experience deluges as intense as the one recorded in 1974. However, within 5 years (2007 and 2011), the Adelaide River floodplain was subjected to two climatic events as extreme as the one recorded in 1974. After the first flood in 2007, rat numbers remained low for 2 years but by 2010 increased to levels recorded during the previous 16 years of the study. However, since the second flood in 2011, rat numbers have not shown any signs of recovery over the subsequent 3 years. Thus, our results demonstrate that an increased frequency of extreme climatic events had a massive long-term negative impact on dusky rat abundance. Importantly, the lack of the python's major prey in seven out of 8 years resulted in dramatic reduction in python feeding rates, significantly reducing python relative body mass, reproductive output, growth rate, body length and survival. Taken together, these proximate demographic factors ultimately resulted in the collapse of the Fogg Dam water python population.

Similar to our results, several recent studies have shown that climate change may have significant multitrophic impacts in other systems (Parmesan 2006; Tylianakis *et al.* 2008; Gilman *et al.* 2010; de Sassi & Tylianakis 2012). For example, long-term plant and animal data from two grassland communities showed that climate sensitivity increased with increasing trophic level (i.e. primary producers, herbivores and carnivores: Voigt *et al.* 2003). These findings led Voigt *et al.* (2003) to suggest that 'the differential trophic sensitivities to climate that we found may indicate a general phenomenon in trophic systems'. The results from the present study, however, do not suggest any significant difference in climate-induced sensitivity among the two tropic levels monitored (dusky rat and water python populations). The discrepancy between the two studies may be caused by the difference in climatic dynamics: the increased trophic level sensitivity observed by Voigt *et al.* (2003) was caused by a gradual shift in mean climatic conditions, whereas in our system, the collapse of the predator prey populations was due to extreme weather events.

Climate-change modelling predicts that by 2030, the wet–dry tropics of Australia will experience both an increase in wet-season rainfall (up to 20%) as well as an increased frequency of extreme climatic events (Eliot, Finlayson & Waterman 1999; Hughes 2003). If these predictions are correct, future climatic conditions might threaten the long-term persistence of the huge biomass of dusky rats and water pythons previously recorded by Madsen *et al.* (2006a,b).

Our results have significant implications for broader issues about the need for long-term data sets to detect population responses to long-term vs. short-term variation in climatic events. Even a 16-year monitoring period was insufficient to capture the significance of two dramatic weather events. That is, any study conducted from 1991 to 2005 would have revealed a relatively stable system dominated by high densities of dusky rats and water pythons (Madsen *et al.* 2006a), albeit fluctuating in response to variation in annual rainfall. Literally overnight, that ecological pattern was obliterated by the massive floods in 2007 and in 2011.

Our study allows us to make a direct comparison between the magnitudes of demographic impact induced by two of the parameters affected by climate change: shifts in annual rainfall, vs. extreme weather events. For both rats and pythons, changes in annual rainfall drove significant temporal shifts in predator–prey abundance (Madsen *et al.* 2006a). In contrast, the two brief deluges in 2007 and 2011 resulted in near-extinction of prey and caused a massive reduction in predator numbers. This sensitivity to

stochastic short-term extreme climatic events makes climate-change impacts exceedingly difficult to predict.

Conclusions

Climate models are more accurate at forecasting shifts in mean conditions, than at predicting the incidence of extreme but localized weather events. Unfortunately, our long-term data on this tropical ecosystem show that wildlife populations may be more sensitive to increased frequency of extreme climatic events than to changes in annual average conditions.

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Data accessibility

All data for this study can be found in the main article and supporting information.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Data from: Floods and famine: climate-induced collapse of a tropical predator-prey community, by Ujvari, Beata; Brown, Gregory; Shine, Richard; Madsen, Thomas