

## How well do predators adjust to climate-mediated shifts in prey distribution? A study on Australian water pythons

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**Abstract.** Climate change can move the spatial location of resources critical for population viability, and a species' resilience to such changes will depend upon its ability to flexibly shift its activities away from no-longer-suitable sites to exploit new opportunities. Intuition suggests that vagile predators should be able to track spatial shifts in prey availability, but our data on water pythons (*Liasis fuscus*) in tropical Australia suggest a less encouraging scenario. These pythons undergo regular long-range (to >10 km) seasonal migrations to follow flooding-induced migrations by their prey (native dusky rats, *Rattus colletti*). However, when an extreme flooding event virtually eliminated rats for a three-year period, the local pythons did not disperse despite the presence of abundant rats only 8 km away; instead, many pythons starved to death. This inflexibility suggests that some vagile species that track seasonally migrating prey may do so by responding to habitat attributes that have consistently predicted prey availability over evolutionary time, rather than reacting to proximate cues that signal the presence of prey per se. A species' vulnerability to climate change will be increased by an inability to shift its activities away from historical sites toward newly favorable areas.

**Key words:** climate change; dusky rats; extreme climatic events; *Liasis fuscus*; predator-prey demography; *Rattus colletti*; spatial heterogeneity; tropical Australia; vagile species; water pythons.

### INTRODUCTION

One significant obstacle to predicting the impacts of climate change is our lack of knowledge of how organisms respond to conditions outside the range they usually encounter. The outcome is easy to predict if climate change exposes organisms to conditions (e.g., of temperature) that exceed their physiological tolerance, but the impacts of less extreme shifts are difficult to foretell. For example, changes in mean values of thermal or hydric conditions, even if they remain within the physiologically tolerable range, may constrain feeding and activity times, and hence, reduce organismal viability (Kearney et al. 2009). Another type of challenge posed by climate change involves the continuing availability of usual conditions, but in places different from where they previously occurred. For example,

warmer weather may result in thermal regimes previously found at low elevations, now being restricted to higher elevations (Deutsch et al. 2008). Whether or not a species can shift to exploit the newly favorable location depends upon factors such as dispersal ability, biotic interactions, and life-history traits (Davis et al. 1998, Pearson and Dawson 2003). For example, a tree species with poorly dispersing seeds may require a long time to colonize a suitable area even close to the original habitat, whereas a vagile species should be more able to exploit an opportunity that emerged in a nearby area.

Because an ability to flexibly respond to shifts in the spatial distribution of resources will enhance a species' resilience in the face of climate change (Pearson and Dawson 2003), we need to incorporate dispersal limitation into our predictions about the impacts of climate change (Peterson et al. 2001). However, predicting the nature of an organism's response to climatically induced spatial redistribution of resources is not simple because redistributions driven by climate change may differ from those driven by other factors. Imagine, for

Manuscript received 23 July 2010; revised 4 August 2010; accepted 20 August 2010. Corresponding Editor: A. M. Bronikowski.

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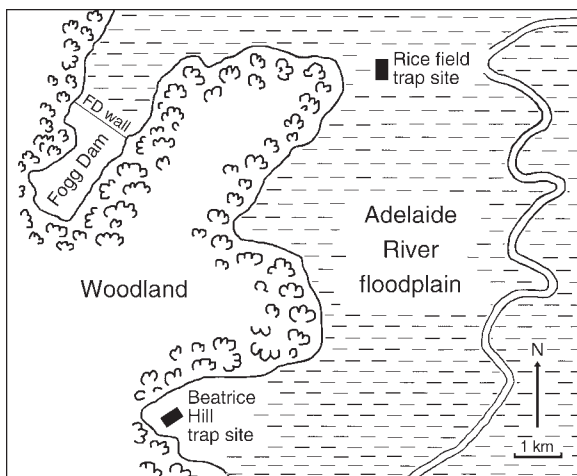


FIG. 1. Map of the study area showing the location of the Fog Dam (FD) wall and the two rat-trapping sites at the Rice Field and Beatrice Hill, ~60 km southeast of Darwin in the Northern Territory of Australia.

example, a predator that shows regular seasonal migrations that keep it in contact with its migrating prey base, a widespread phenomenon (e.g., migrating herds of African ungulates are accompanied by lions, cheetahs, and hyenas; Schaller 1972). Intuition suggests that such predators will readily surmount the challenges of locating prey even if climate change modifies its location because mobility to maintain foraging opportunities is a central feature of the species' ecology (Peterson et al. 2001). That prediction may be in error if consistent correlations between seasonal prey distributions and habitat features through evolutionary time favor reliance on (invariant) habitat features rather than (variable) prey numbers as the proximate cues for predator movements. Our field studies on water pythons (*Liasis fuscus*) suggest such a scenario, whereby individuals of a vagile, seasonally migratory predator reacted to a sudden decrease in prey availability not by moving to a nearby area where food was abundant, but by remaining in their usual home ranges and (in many cases) starving to death.

## MATERIALS AND METHODS

### *Study area and species*

Our study area is ~60 km southeast 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; Madsen et al. 2006). The Adelaide River floodplain is a flat, treeless area formed by silt

deposition, and the vegetation consists primarily of native sedges and grasses.

Water pythons (see Plate 1) are large (to 3 m) nonvenomous snakes widely distributed across tropical Australia (Cogger 2000). The results in the present study are based on a capture-mark-recapture study of pythons collected on the Adelaide River floodplain at two sites: (1) between August to December from 1991 to 2009 on a 1.3 km long dam wall at Fog Dam Conservation Reserve (mean number of days of fieldwork = 66 d/yr, range 36 to 105; however, no fieldwork was conducted in 2004 or 2006) and (2) during four nights in November 2009 on a 1.3 km long dam wall at Beatrice Hill, 8 km southeast of the Fog Dam wall (Fig. 1).

After being captured at night by spotlighting, the snakes were individually marked (by ventral scale clipping) and snout-vent length (SVL), mass, and female reproductive status (i.e., gravid vs. non-gravid; see Madsen and Shine 1996a) were recorded. Prey records were obtained by palpation and by fecal analyses. All snakes were released within 24 h after being captured.

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. 2006). Demographic data on rats were derived from 5-d trapping periods in August (mid-dry season) at two sites. Because the floodplain close to the Fog Dam wall is often inundated in August, our first trap site was situated 5 km northeast of Fog Dam, in an area formerly used for rice production ("Rice fields"; Fig. 1). This site was trapped from 1991 to 2009 (except for 2004 and 2006). Data from previous years of monthly trapping at Fog Dam and at the Rice fields show that rat numbers at the two sites are highly correlated ( $r = 0.63$ ,  $P = 0.0003$ ,  $df = 27$ ; Madsen and Shine 1999). Furthermore, the Rice field site is situated in the general area to which the Fog Dam water pythons migrate during the wet season (Madsen and Shine 1996b, 1998). Our second site, at Beatrice Hill, 8 km south of the Rice field site, was situated close to higher ground (<200 m from Beatrice Hill; Fig. 1). At both sites, we deployed 50 Elliott traps placed at 10-m intervals along a 500-m transect. The traps were baited with rolled oats, and at the Rice field site placed at same positions during each year. Each rat was given an individually numbered ear tag prior to release so that our counts of rat abundance do not include repeated captures of the same individual.

The reason for using the additional trapping site at Beatrice Hill was the serendipitous discovery of large number of rats at this site by a local farmer. The abundance of rats at this site was in striking contrast to their virtual disappearance over all other areas on the Adelaide River floodplain after the flood in 2007 (see *Results*).

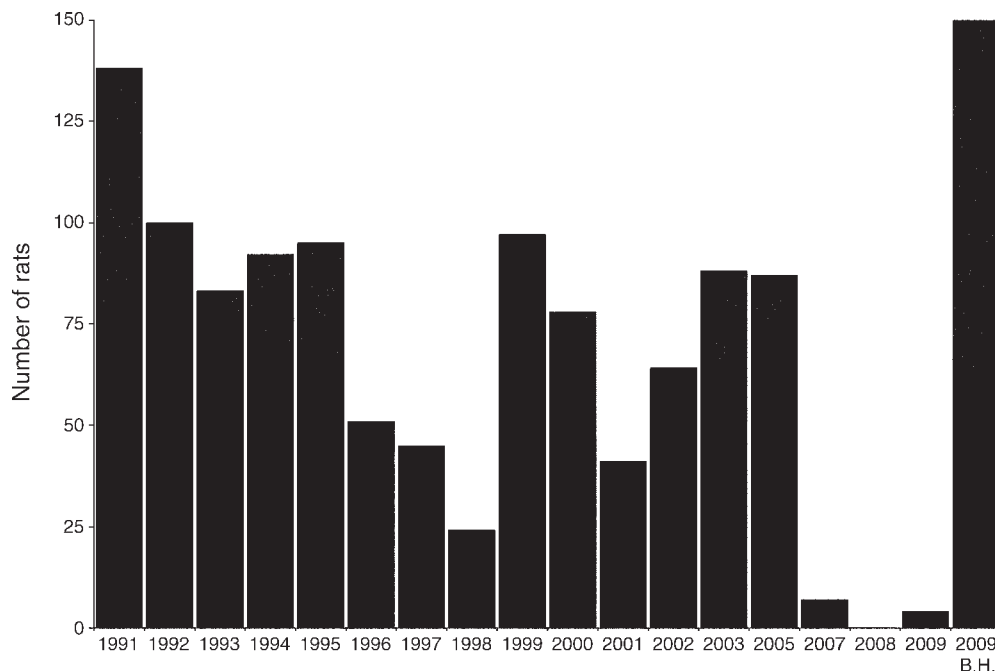


FIG. 2. Number of dusky rats (*Rattus colletti*) captured at the Rice Field trap site from 1991 to 2009. Data from rats trapped at Beatrice Hill in 2009 are denoted by B.H.

#### *The inland tsunami of March 2007*

Monsoonal rainfall inundates most of the Adelaide River floodplain every wet season, but the increase in water levels is typically a gradual process. On 3 March 2007, however, 244 mm of rain fell within 24 h in the Adelaide River catchment (the highest daily rainfall recorded at Adelaide River Post meteorological station since records began in 1956). Flooding down the Adelaide River from this massive rainfall event coincided with a high tide, preventing the water from flowing out to the sea. The result was an “inland tsunami” (a tidal wave with a height of  $\sim 1$  m) that reached our study sites in the morning of 7 March (P. Fisher, *personal communication*). Within a few hours, the entire Adelaide River floodplain was underwater.

#### *Statistical analyses*

Data were examined for normality before analysis, and we used nonparametric methods if normality could not be achieved. Analyses were carried out using JMP version 5.1 (SAS institute 1998). In order to quantify among-year variation in python relative body mass, we calculated residual body mass (henceforth RBM) from a general linear regression of ln-transformed mass on ln-transformed SVL (excluding gravid pythons and snakes with freshly ingested prey). We used the Jolly-Seber model available in POPAN-5 (Arnason and Schwarz 1999) to estimate the numbers and survival of Fogg Dam water pythons.

#### RESULTS

Even in the years prior to the inland tsunami (1991–2005), the total number of rats captured at the Rice Field trap site varied significantly among years, ranging from 24 in 1997 to 138 in 1991 (Kruskal-Wallis test  $T_{13} = 58.32$ ,  $P < 0.0001$ ; Fig. 2). However, the tsunami of March 2007 dramatically reduced rat abundance, and only seven rats were captured along the transect in 2007, none in 2008, and four in 2009 (Fig. 2). In contrast, in 2009 150 rats were trapped at the Beatrice Hill site, more than we ever recorded at the Rice Fields site trapping sessions since 1991 (Fig. 2).

Reflecting the high rat numbers at Beatrice Hill, the proportion of freshly captured snakes containing prey was higher at that site (47 of 72; 65.3%) than at Fogg Dam (16 of 124, 12.9%;  $\chi^2 = 54.9$ ,  $P < 0.0001$ ,  $df = 1$ ). Dietary composition also differed. All of the 47 pythons captured with prey at Beatrice Hill in 2009 had been feeding on dusky rats. In contrast, the emaciated pythons at Fogg Dam in 2009 had a far broader diet: Of 16 animals with prey, only five had been feeding on rats, with the remaining 11 snakes taking lizards and other snakes.

As expected, if python RBM is driven by feeding rates, water python RBM varied among years ( $F_{17,4156} = 66.71$ ,  $P < 0.0001$ ; Fig. 3) and in concert with rat numbers ( $r^2 = 0.86$ ,  $P < 0.0001$ ,  $df = 17$ ; Fig. 4), strongly suggesting that temporal variation in python RBM is driven by food (rat) availability in this system. A post

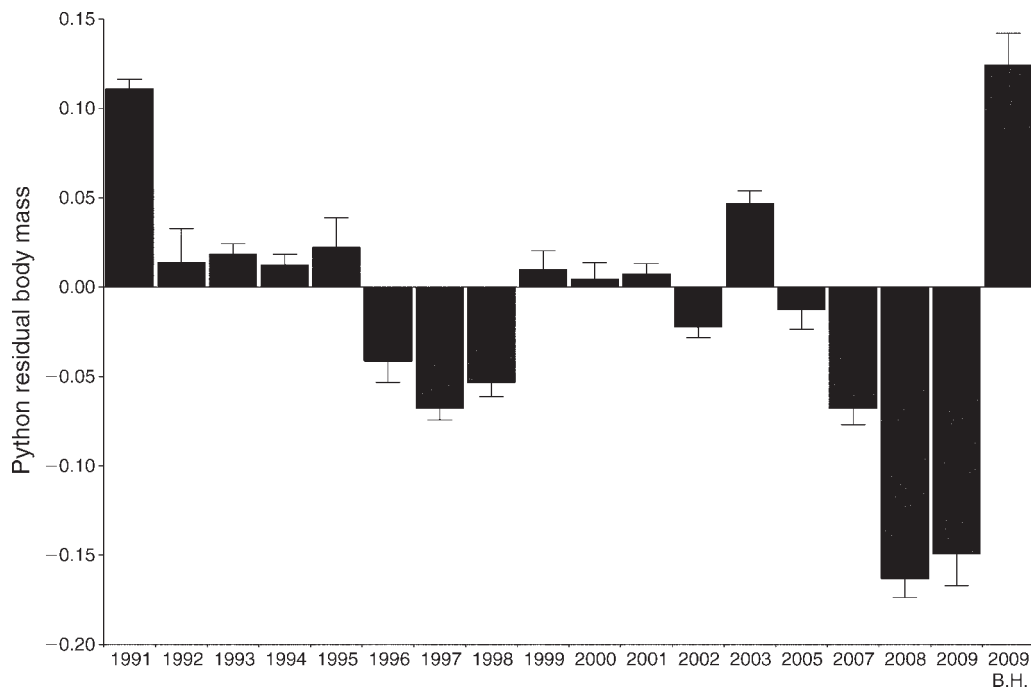


FIG. 3. Residual body mass (RBM; mean  $\pm$  SE) of water pythons (*Liasis fuscus*) captured at the Fogg Dam wall from 1991 to 2009. RBM was calculated from a general linear regression of ln-transformed mass on ln-transformed snout–vent length (excluding gravid pythons and snakes with freshly ingested prey). Data from pythons captured at Beatrice Hill in 2009 are denoted by B.H.

hoc Tukey-Kramer hsd test showed that the mean RBM of the pythons captured at the Beatrice Hill site in 2009 was significantly higher than that of pythons captured at the Fogg Dam wall during any year of our 19-year study at that site. In contrast, in 2008 and 2009 RBM of pythons at Fogg Dam was lower than we have recorded at any other time during our long-term study (Fig. 3). Many animals were so emaciated that they were virtually unable to move, and in 2009 six animals died within a few hours of capture (none of the snakes captured at Beatrice Hill died after being captured). The low prey abundance and concomitant low RBM of Fogg Dam pythons dramatically reduced annual survival rates, and between 2008 and 2009 survival dropped to 42%, considerably lower than the annual survival rates recorded between 1987 and 2003 (mean = 79%, range 60–94%; Madsen et al. 2006). Reflecting the low RBM of the Fogg Dam pythons, no gravid females were captured in 2008 and 2009 (compared to a mean of 51%, range 8.8–87.2%, recorded between 1990 and 2003; Madsen et al. 2006). The lack of reproductive females in 2008 resulted in no recruitment of yearling pythons being recorded in 2009.

Python population size at Fogg Dam in 2007 was estimated to  $2183 \pm 197$  (estimation  $\pm$  SE) snakes, similar to estimates recorded from 1988 to 2002 (Madsen et al. 2006). In 2008, estimated python numbers decreased to  $1434 \pm 175$  snakes, and in 2009

the estimated number fell dramatically to  $536 \pm 106$  snakes, the lowest ever recorded during our long-term study at Fogg Dam (Madsen et al. 2006). Our samples of pythons from Fogg Dam vs. Beatrice Hill also differed in the proportion of recaptured animals (i.e., that had been marked prior to that year). Of 124 pythons captured at the Fogg Dam wall in 2009, 33 (26.6%) were recaptures from previous years, whereas all of the 72 pythons captured at Beatrice Hill were unmarked (comparing the two sites,  $P < 0.0001$ , Fisher's exact test).

#### DISCUSSION

Although stochastic variation in monsoonal rainfall generates substantial temporal variation in this system, broad patterns of floodplain inundation, and rodent and snake responses to that inundation, have been consistent throughout our long-term study (Madsen and Shine 1996b, 1999, Madsen et al. 2006). Wet-season rainfall raises the water table, causing flooding, and levee banks along the main river channel provide the only high ground that remains dry during a normal wet season (Madsen and Shine 1996b, 1999). Dusky rats aggregate on this high ground, and water pythons migrate to such areas to feed on the rodents (Madsen and Shine 1996b, 1999). This situation changed dramatically in March 2007, when a combination of torrential rain upstream and a high tide produced a 1-m tsunami that inundated

the entire floodplain, including the levee banks. Although we cannot attribute specific events such as this one to climate change, it is an example of the kind of extreme weather events likely to increase in frequency and severity with global warming (Hughes 2000, Easterling et al. 2000).

Our data suggest that virtually all rats at the Rice Field site were drowned by this catastrophic event. Although unique in our own study, earlier research on rats at the Adelaide River floodplain reported a similar phenomenon: 250 mm of local rain on 4 December 1974 was followed by a cyclonic deluge on 24 December of the same year (Redhead 1979). Coincident with the massive flood resulting from those events, the numbers of dusky rats recorded by Redhead (1979) plummeted from high levels in 1972 through 1974 to zero in 1975, and only three rats were trapped in 1976. Redhead (1979) attributed the disappearance of rats to drowning. Although the inland tsunami caused massive mortality of rodents in most areas of the Adelaide River floodplain, rats living along the floodplain edges (such as the Beatrice Hill site) survived by moving up to adjacent higher ground. Hence, rapidly rising water levels were catastrophic for rats at the Rice fields (and the area trapped by Redhead in 1974, 10 km northwest of the Rice Field site), but did not imperil conspecifics close to the higher ground at Beatrice Hill. The resultant spatial divergence in rat abundance generated corresponding divergence in python feeding rates and RBM. Indeed, the spatial divergence in these traits between these two nearby sites in 2009 was more extreme than the temporal divergence we have recorded during our 19-year study at Fogg Dam, despite significant variation in climatic conditions over that period.

Clearly, conditions for water pythons were far better at Beatrice Hill than at Fogg Dam after the tsunami-induced destruction of the python's prey resource in 2007. Remarkably, however, the Fogg Dam pythons appear to have remained in their usual area, where a virtual absence of rodent prey forced the snakes to eat a wider range of foods, to eat less often, and hence, to become increasingly emaciated. We do not have direct proof that the dramatic reduction in python numbers at Fogg Dam was solely due to starvation-induced mortality, as the lack of recruitment will also have contributed to this decline. However, several patterns (the lack of prey, the highly emaciated animals, the strong relationship between python RBM and survival [Madsen et al. 2006], frequent deaths of freshly caught animals, the lack of reproductive females and the increased mortality between 2008 and 2009) all suggest that increased mortality was a major cause of the dramatic decline in python numbers in 2009. This scenario is supported by other studies on snakes such as European adders (*Vipera berus*), Texas ratsnake (*Elaphe obsoleta*) and Arafura filesnakes (*Acrochordus*

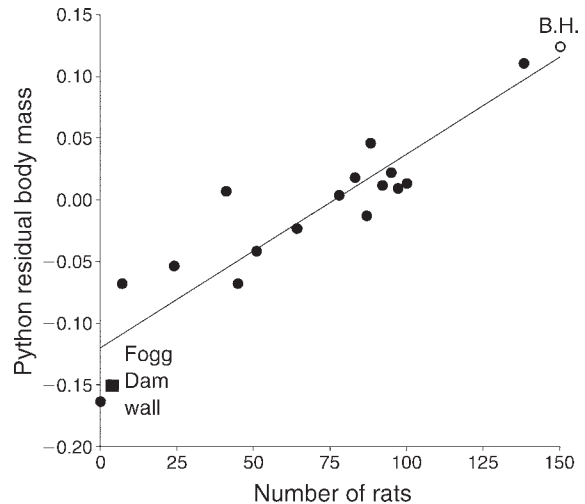


FIG. 4. Relationship between variation in rat abundance and variation in residual body mass of water pythons captured on the Fogg Dam wall from 1991 to 2009 (solid circles). The open circle denotes 2009 data for the number of rats captured at Beatrice Hill (B.H.) and body condition of pythons captured at Beatrice Hill. The solid square shows 2009 data for the number of rats captured at the Rice Field and residual body mass of pythons captured on the Fogg Dam wall.

*arafurae*), where dramatic reductions in prey availability caused snake emaciation and increased mortality resulting in subsequent crashes in population size (Madsen and Stille 1988, Sperry and Weatherhead 2008, Ujvari et al. 2010).

Why did the Fogg Dam pythons not disperse to greener pastures? In many species, dispersal is constrained by factors such as low vagility, a lack of suitable dispersal corridors, and/or behavioral exclusion by conspecifics already resident in the area that offers better foraging opportunities (Pearson and Dawson 2003). None of these factors are relevant to water pythons. First, water pythons exhibit annual wet-season migrations to high ground (levee banks) in pursuit of dusky rats (Madsen and Shine 1996b). The distances covered in those seasonal migrations are often >10 km, greater than the distance between the Beatrice Hill site and Fogg Dam. Second, the habitat between these two areas is suitable for pythons; there is no physical or ecological barrier that would inhibit snake movement (Madsen and Shine 1998). Third, water pythons do not display any territorial defense (Madsen and Shine 1996b, 1998), so social barriers to migration likely are trivial or nonexistent.

Dispersal away from food-poor areas may, however, be constrained by the strong dry-season philopatry of these snakes. Although individual pythons migrate long distances during the wet season each year, radiotelemetry shows that all return to previous haunts each dry season when the floodwaters subside (Madsen and Shine



PLATE 1. Dusky rats (*Rattus colletti*) normally constitute the main prey for water pythons (*Liasis fuscus*) living on the Adelaide River floodplain, Australia. However, in March 2007, an inland tsunami inundated most of the floodplain resulting in a dramatic reduction in rat numbers for the pythons living at Fogg Dam Conservation Reserve. In order to survive, the snakes had to start feeding on alternative prey. The photo above shows a juvenile water python feeding on such an alternative prey, an adult dragon lizard (*Lophognathus* sp.). Photo credit: Gregory Brown.

1996b, 1998). Thus, high vagility during the wet season is replaced by strong philopatry and relatively sedentary behavior during the dry season. In other work, we have shown a very low rate of dry-season intermingling among pythons from areas of the floodplain <3 km apart (Madsen and Shine 1998). Given that we have marked and released >5900 water pythons at Fogg Dam over the course of our study, and that these are long-lived animals (often >10 years; Ujvari and Madsen 2009), the absence of marked individuals at Beatrice Hill strongly suggest that the Fogg Dam snakes did not migrate to Beatrice Hill. The emaciated snakes captured at Fogg Dam in 2008 and 2009 suggest that they were unable to find prey in other areas of their wet-season hunting grounds on the Adelaide River floodplain. The widespread scarcity of rats was confirmed by a large (>10-person) research group during their routine field work along the network of roads and tracks that crisscross the floodplain.

Seasonal migrations by predators that track prey movements across the landscape may be driven by a variety of proximate cues. At one extreme, predators assess prey abundance using information from the prey themselves (Schaller 1972). At the other extreme, prey availability may correlate so consistently with habitat features that predators use cues from those latter features to predict feeding opportunities. This is clearly the case with seasonal migrations that cover distances so vast that no cues from the destination site are available to the migrating animals for most of their journey (e.g., whales, passerine birds; Lockyer and Brown 1981, Dingle 1996). If water pythons similarly use seasonal “dispersal rules” based on habitat features, then a shift in the usual patterns of correlation between landscape features and prey availability may pose significant challenges. Such a shift certainly occurred after the tsunami at our Rice Field study site, and such extreme climatic events are predicted to occur more often in the

future (Easterling et al. 2000). Our results strongly suggest that an ability for populations to accurately track changes in the spatial distribution of resources should not be assumed; even highly mobile predators may prove surprisingly inept at locating and exploiting superficially “available” resources that are located in areas close to those in which they have previously occurred. Strong spatial structure in gene frequencies within populations hints that dispersal rates often may be low, even in animals that are physically capable of traveling large distances (Koenig et al. 1996, Dubey et al. 2008). Hence, climate-driven changes in the spatial location of resources may prove a substantial challenge for many organisms, and the availability of apparently suitable areas may not be enough to prevent significant population declines even in vagile taxa.

#### ACKNOWLEDGMENTS

We thank Eric Cox for pointing out the abundance of dusky rats at Beatrice Hill. The research was supported by grants from the National Geographic Society and the Australian Research Council. The work was conducted under University of Wollongong animal ethics approval number AE04/03 and Parks and Wildlife Commission of the Northern Territory permit number 21940.

#### LITERATURE CITED

- Arnason, A. N., and C. J. Schwarz. 1999. Using POPAN-5 to analyse banding data. *Bird Study* 46:S157–S168.
- Cogger, H. 1992. *Reptiles and amphibians of Australia*. Reed Books, Sydney, Australia.
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391:783–786.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA* 105:6668–6672.
- Dingle, H. 1996. *Migration. The biology of life on the move*. Oxford University Press, Oxford, UK.
- Dubey, S., G. P. Brown, T. Madsen, and R. Shine. 2008. Male-biased dispersal in a tropical Australian snake (*Stegonotus cucullatus*, Colubridae). *Molecular Ecology* 17:3506–3514.
- Easterling, D. R., J. L. Evans, P. Ya. Groisman, T. R. Karl, K. E. Kunkel, and P. Ambenje. 2000. Observed variability and trends in extreme climate events: a brief review. *Bulletin of the American Meteorological Society* 81:417–425.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15:56–61.
- Kearney, M. R., W. Porter, and R. Shine. 2009. The potential for behavioral thermoregulation to buffer ‘cold-blooded’ animals against climate warming. *Proceedings of the National Academy of Sciences USA* 106:3835–3840.
- Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* 11: 514–517.
- Lockyer, C. H., and S. G. Brown. 1981. The migration of whales. Pages 105–137 in D. J. Aidley, editor. *Animal migration*. Cambridge University Press, Cambridge, UK.
- Madsen, T., and R. Shine. 1996a. Determinants of reproductive output in female water pythons (*Liasis fuscus*, Pythonidae). *Herpetologica* 52:146–159.
- Madsen, T., and R. Shine. 1996b. Seasonal migration of predators and prey, a study of pythons and rats in northern Australia. *Ecology* 77:149–156.
- Madsen, T., and R. Shine. 1998. Spatial subdivision of tropical pythons (*Liasis fuscus*) in a superficially homogenous habitat. *Australian Journal of Ecology* 23:340–348.
- Madsen, T., and R. Shine. 1999. Rainfall and rats on a tropical floodplain: Climatically-driven dynamics of an Australian rodent population. *Australian Journal of Ecology* 24:80–89.
- Madsen, T., and B. Stille. 1988. The effect of size dependent mortality on colour morphs in male adders, *Vipera berus*. *Oikos* 52:73–78.
- Madsen, T., B. Ujvari, R. Shine, and M. Olsson. 2006. Rain, rats and pythons: climate driven population dynamics of predators and prey in tropical Australia. *Austral Ecology* 31: 30–37.
- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361–371.
- Peterson, A. T., V. Sanchez-Cordero, J. Soberon, J. Bartley, R. W. Buddemeier, and A. G. Navarro-Singuenza. 2001. Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecological Modelling* 144:21–30.
- Redhead, T. D. 1979. On the demography of *Rattus sordidus colletti* in monsoonal Australia. *Australian Journal of Ecology* 4:115–136.
- SAS Institute. 1998. *JMP version 5.1*. SAS Institute, Cary, North Carolina, USA.
- Schaller, G. B. 1972. *The Serengeti lion*. Chicago University Press, Chicago, Illinois, USA.
- Sperry, J. H., and P. J. Weatherhead. 2008. Prey-mediated effects of drought on condition and survival of a terrestrial snake. *Ecology* 89:2770–2776.
- Ujvari, B., S. Andersson, G. Brown, R. Shine, and T. Madsen. 2010. Climate-driven impacts of prey abundance on the population structure of a tropical predator. *Oikos* 119:188–196.
- Ujvari, B., and T. Madsen. 2009. Short telomeres in hatchling snakes: Erythrocyte telomere dynamics and longevity in tropical pythons. *PLoS ONE* 4:e7493.