Climate-induced reaction norms for life-history traits in pythons

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Abstract. Climate change modelers predict increasingly frequent “extreme events,” so it is critical to quantify whether organismal responses (such as reproductive output) measured over the range of usual climatic conditions can predict responses under more extreme conditions. In a 20-year field study on water pythons (Liasis fuscus), we quantified the effects of climatically driven annual variation in food supply on demographic traits of female pythons (feeding rate, body size, body mass, and reproductive output). Reaction norms linking food supply to feeding rates and residual body mass were broadly linear, whereas norms linking food supply to female body size became curvilinear when a dramatic (flooding-induced) famine reduced the mean body size at sexual maturity. Thus, the 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.

Key words: dusky rat; extreme climatic events; food supply; Liasis fuscus; life-history plasticity; phenotypic plasticity; Rattus colletti; reaction norms; snake; tropical Australia; water python.

INTRODUCTION

In their natural environments, most organisms experience stochastic variation in resource availability. Such variation often induces shifts in behavior and ecology, either as a direct result of the environmental pressure (e.g., less food results in slower growth) or an adaptively fashioned response (e.g., increased allocation of energy to long-term storage in the face of a less predictable food supply; Madsen and Shine 2000). Accordingly, the life-history traits of any given population can be quantified not simply as mean values and ranges of the relevant traits (e.g., body size and age at maturation, and reproductive output), but also as norms of reaction that link variation in environmental conditions to variation in expression of those traits (Stearns and Koella 1986). For example, stochastic variation in annual rainfall patterns in the Australian wet–dry tropics massively influences rates of growth, survival, and reproduction of many organisms living in that region (Madsen et al. 2006, Ujvari et al. 2010).

Reaction norms for life-history traits may determine a population’s response to variation in environmental conditions. Thus, understanding life-history plasticity is central to predicting population responses to changing environments, such as are predicted under models of anthropogenically caused global warming (Easterling et al. 2000). Although it is relatively straightforward to model such reaction norms, measuring them in the field is a greater challenge. We need long-term studies that document population responses to a wide range of conditions, ideally spanning the parameter values predicted to occur under climate change models (Easterling et al. 2000). If climate change results in environmental conditions outside the “envelope” experienced over historical records (as may well occur; Easterling et al. 2000), then it may be difficult to predict population responses to more extreme/novel perturbations (Ghalambor et al. 2007).

In the present paper, we describe and analyze a 20-year (see Supplement) set on prey abundance and life-history traits (feeding rates, body mass, growth rates, body sizes, and age and size at maturation) of free-ranging female water pythons (Liasis fuscus; see Plate 1) in tropical Australia. Earlier work on this population has shown that annual rainfall patterns strongly affect food supply, and thus python life-history traits (Madsen et al. 2006). In 2007, however, an extreme weather event...
Materials and Methods

Study area and species

The Fogg Dam Conservation Reserve lies ~60 km southeast of Darwin in the Northern Territory of Australia, within the “wet–dry” tropics (13°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–March (Madsen et al. 2006).

Water pythons are large (to 3 m) nonvenomous snakes widely distributed across tropical Australia (Cogger 2000). Results in the present study are based on a capture-mark–recapture study of female pythons conducted July–October from 1991 to 2010 at Fogg Dam Conservation Reserve. However, no fieldwork was conducted in 2004 or 2006, and in 2005 the fieldwork did not include the months when female pythons are reproductive. Our analysis is based only on females, because we cannot accurately score the reproductive status of male pythons.

After capturing the snakes at night by spotlighting, we individually marked them (by scale-clipping) and recorded body size (snout–vent length, SVL), mass, and female reproductive status (i.e., reproductive vs. nonreproductive; see Madsen and Shine 1996). The reproductive cycle of the pythons in our study area is highly synchronous, with mating in July–early August, oviposition September–October, and hatching from mid-November to early December (Madsen and Shine 1996). Reproductive (pre-ovulatory, reproductive, or immediately post-ovipositional) females are easily recognizable by body shape during July–October (Madsen and Shine 1996). Data on clutch sizes used in this paper were based on 111 females that oviposited in the laboratory in 1991 and 1992, and from 17 of the 42 reproductive females captured in 2010 for which (due to their small size) we were able to accurately document clutch size by abdominal palpation.

Our analyses on the age of female pythons are based on a subset of marked snakes for which we could confidently infer the age of each snake. These animals fall into two groups: (1) offspring from eggs that we hatched in captivity (n = 1448), so that we knew the exact date of hatching, and (2) hatchlings and juveniles that were collected in the field at such a small body size that they could be unequivocally allocated to a given age class (n = 632; Madsen and Shine 2000). To quantify annual variation in relative female growth rates, we used residual scores from linear regression of annual growth rate to mean snout–vent length (the latter based on mean snout–vent length over the interval between first and second capture). In order to estimate among-year variation in python body mass, we calculated residual body mass scores (henceforth RBM) from a general linear regression of ln-transformed mass on ln(SVL). Snakes with newly ingested prey were not included in the analysis. To quantify annual minimum body sizes at female maturation, we calculated the mean SVL of the 20% smallest reproductive female pythons.

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 five-day trapping periods in August (middle of the dry season) at a site 5 km northeast of Fogg Dam. This site was trapped each year from 1991 to 2010 (except for 2004 and 2006). We deployed 50 Elliott traps placed at 10-m intervals along a 500-m transect. The traps were baited with rolled oats and were placed at the same positions 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 inland tsunami of March 2007

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 within 24 h in the Adelaide River catchment (the highest daily rainfall recorded at Adelaide River Post meteorological station since records began in 1956). The consequent flooding down the Adelaide River resulted in an “inland tsunami” (a tidal wave with a height of ~1 m) that reached our study sites on 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 conducted using JMP version 5.1 (SAS Institute 1998). Time series of population parameters from a given site are strongly serially dependent (Weatherhead et al. 2002). We therefore obtained significance values of the $F$ statistic by randomization trials in the following time series analyses: number rats, python RBM, growth rates, and body length of gravid females and of the 20% of the smallest gravid females. We randomized the order of the variable on the $x$-axis (years), kept the order of the
variable on the y-axis (variables) constant, and calculated the statistics of interest by running 10,000 randomizations. We then compared the slope of the correlation for the data in their true order to the family of values obtained from the 10,000 randomization trails to derive a P value.

To determine whether reaction norms were best described by linear or curvilinear relationships, we relied on a model selection approach based on the Akaike information criterion, AIC (Burnham and Anderson 2002), according to the following formula:

$$\text{AIC} = -2 \log \text{Likelihood} + 2K$$

where $K$ is the number of parameters (number of variables + 1 to include the intercept; Sugiura 1978).

The relative performance of alternative models was measured using the delta AIC:

$$\Delta \text{AIC} = \text{AIC}_i - \min \text{AIC}$$

where $\text{AIC}_i$ is the AIC value for model $i$, and $\min \text{AIC}$ is the AIC value (minimum) of the best-fitting model. Hence, the difference between the AIC scores of the various models ($\Delta \text{AIC}$) provides a measure of the relative reliability of the competing models. The advantage of this approach is that it allows for ranking various competing models based on their relative likelihood, and does not rely on any threshold value (alpha level; Vapnik 2000). The AIC penalizes the addition of parameters, and hence selects a model using a minimum number of parameters according to the principle of simplicity and parsimony (Akaike 1973); therefore, models with lowest $\Delta \text{AIC}$ were selected.

**RESULTS**

Annual variation in prey and female python ecology

All of the characteristics that we measured varied considerably among years; analyses were based on Monte Carlo simulations, which do not provide df values. Numbers of dusky rats trapped annually differed significantly, from none in 2008 to 138 in 1991 (randomization test: $F = 38.298$, simulated $F = 1.015$, variance of simulated indices = 0.158, $P < 0.0001$; Fig. 1a). We also recorded substantial annual variation in feeding rates (the percentage of female pythons containing freshly ingested prey ranged from 4.1% in 2009 to 38.9% in 1991; Fig. 1b), residual body mass ($F = 87.041$, simulated $F = 11.332$, variance of simulated indices = 0.265; $P < 0.0001$; Fig. 1c), annual residual growth rates ($F = 6.457$, simulated $F = 1.016$, variance of simulated indices; $P < 0.0001$; Fig. 1d), and mean body size (snout–vent length) of reproductive females ($F = 22.874$, simulated $F = 0.991$; variance of simulated indices = 0.150; $P < 0.0001$; Fig. 1e), and of the smallest 20% of reproductive females ($F = 13.81$, simulated $F = 0.984$, variance of simulated indices = 0.146, $P < 0.0001$; Fig. 1e).

A post hoc Tukey-Kramer post hoc test revealed that in 2008 and 2009, female pythons exhibited lower mean residual body mass (Fig. 1c) and lower growth rates (Fig. 1d) than in previous years. The same test revealed that the mean body lengths of all reproductive females and of the smallest 20% of reproductive females were significantly lower in our 2010 sample than in any other years (Fig. 1e). The low mean body size of reproductive females in 2010 (mean SVL = 143.5 cm, mean mass = 1317 g, $n = 42$) is in stark contrast to the values recorded over the previous 16 years for the same population (mean SVL = 176.3 cm, mean mass = 2190 g, $n = 969$).

Clutch sizes of water pythons are highly correlated with maternal body size (Madsen and Shine 1996). Although clutches of the 2010 females were small in absolute terms, they were consistent with the relationship between maternal body size and clutch size seen in earlier years (ANOVA with year as a factor, clutch size as dependent variable, and SVL as covariate: $F_{1,125} = 2.67, P = 0.11$; Fig. 1f).

Reaction norms

Our earlier studies on this system (1988–2002) suggested that annual variation in python life-history traits is driven primarily by the abundance of their main prey, dusky rats, which in turn is driven by patterns of rainfall late in the wet season (Madsen et al. 2006). In contrast to the previous 16-year study, rats were virtually eliminated by the flood in March 2007 (7 rats captured in 2007, 0 in 2008, 4 in 2009), and the rat population took about three years to recover (62 rats captured in 2010: Fig. 1a). Thus, the present study expands the range of rat abundance levels over which python responses can be assessed.

Similar to our previous results (Madsen et al. 2006), we observed a significant positive relationship between the feeding rates of snakes (annual percentage of female pythons with prey) and annual rat numbers (Fig. 2a, $r_{16} = 0.84, P < 0.0001$; the $\Delta \text{AIC}$ criterion in Table 1 suggested that these data were better fitted by a linear than a curvilinear model) as well as female residual body mass (Fig. 2b, $r_{16} = 0.82, P < 0.0001$; again the $\Delta \text{AIC}$ criterion in Table 1 supported a linear model). Female pythons also grew more slowly in years when rats were less abundant (Fig. 2c, $r_{13} = 0.91, P < 0.0001$; in contrast to the previous two analyses, the $\Delta \text{AIC}$ criterion in Table 1 suggested that a curvilinear model provided a better fit than a linear model). The slow growth rates of female pythons after the flood (i.e., 2007–2010) resulted in much smaller age-specific body sizes than in any other years of our study. For example, three four-year-old females that initiated reproduction in 2010 were similar in size (body lengths of 129, 131 and 135 cm) to two-year-old females that grew up during previous years with a more abundant food supply (Madsen and Shine 2000).
The relationship between rat abundance and mean body size of snakes is more complex, in that an animal’s current body size is driven by growth rates (and hence, food availability) over previous years as well as the current year. Thus, we calculated mean rat abundance over the three previous years (the average time period for a female hatchling python to initiate reproduction; Madsen and Shine 2000), as the independent variable for these analyses. This measure of mean prey availability was significantly correlated with the mean body length of reproductive females each year (Fig. 2d, \( r_{11} = 0.73, P = 0.0044 \); the \( D_AIC \) criterion in Table 1 suggested that the relationship was curvilinear rather than linear) and with mean SVL of the smallest 20% of reproductive females (Fig. 2e, \( r_{11} = 0.76, P = 0.0029 \); the \( D_AIC \) criterion in Table 1 suggested a curvilinear rather than linear relationship). However, annual variation in prey availability was not significantly linked to mean body sizes of nonreproductive female pythons (Fig. 2f, \( r_{11} = 0.22, P = 0.44 \)). The curvilinear reaction norms depicted in Fig. 2c, d, and e were a result of the low prey abundance in 2007–2009, resulting in substantial reduction in annual growth rates, as well as in mean and minimum body sizes of reproductive female pythons in 2010. This conclusion is supported by analyses excluding data from this unusual event: if we omit the years postflood, the \( AIC \) criteria support a linear rather than curvilinear reaction norm (Table 1).

**DISCUSSION**

Our 20-year data set on water python ecology confirms strong links between prey availability and
TABLE 1. Akaike information theory criteria for model fit of linear vs. curvilinear models as explanations for reaction norms linking annual variation in prey abundance to water python (*Liasis fuscus*) life-history traits.

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Linear model</th>
<th></th>
<th>Curvilinear model</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AIC</td>
<td>ΔAIC</td>
<td>AIC</td>
<td>ΔAIC</td>
</tr>
<tr>
<td>Percentage with prey vs. number of rats</td>
<td>561.38</td>
<td>0</td>
<td>565.87</td>
<td>4.49</td>
</tr>
<tr>
<td>RBM vs. number of rats</td>
<td>4.88</td>
<td>0</td>
<td>7.90</td>
<td>3.02</td>
</tr>
<tr>
<td>Annual growth vs. number of rats</td>
<td>13.32</td>
<td>5.08</td>
<td>8.24</td>
<td>0</td>
</tr>
<tr>
<td>Mean SVL of gravid females vs. mean number of rats</td>
<td>361.30</td>
<td>7.12</td>
<td>354.18</td>
<td>0</td>
</tr>
<tr>
<td>Mean SVL of smallest 20% of gravid females vs. mean number of rats</td>
<td>174.11</td>
<td>4.74</td>
<td>169.37</td>
<td>0</td>
</tr>
<tr>
<td>Annual growth vs. no. rats (years of low rat abundance excluded, i.e., 2007–2009)</td>
<td>5.34</td>
<td>0</td>
<td>9.05</td>
<td>3.71</td>
</tr>
<tr>
<td>Mean SVL gravid females vs. mean number of rats (2010 excluded)</td>
<td>223.39</td>
<td>0</td>
<td>225.88</td>
<td>2.49</td>
</tr>
<tr>
<td>Mean SVL of smallest 20% of gravid females vs. mean no. rats (2010 excluded)</td>
<td>206.45</td>
<td>0</td>
<td>209.91</td>
<td>3.46</td>
</tr>
</tbody>
</table>

Notes: ΔAIC scores result from fitting linear vs. curvilinear models to reaction norms depicted in Fig. 2. The best-fitting model for each relationship is in boldface font. RBM stands for residual body mass; SVL stands for snout–vent length.
predator (python) demography (as suggested by earlier work on this system; Madsen et al. 2006), but also offer a strong cautionary tale. When prey availability (dusky rat abundance) was dramatically reduced by an extreme climatic event that resulted in unprecedented flooding, the female pythons responded by reproducing at body sizes far below any that we had documented over the previous 16 years. Quantitative relationships between prey availability and python reproductive responses under extreme food deprivation thus were not predictable from our previous 16 years of fieldwork conducted under "normal" (but nonetheless, highly variable) climatic conditions.

The mechanistic basis for the effects documented in Fig. 2 is relatively straightforward. Annual variation in late wet-season rainfall drives vegetation growth (food supply) and habitat availability for dusky rats (Madsen et al. 2006). More rats mean more food for pythons, and more food means more energy for pythons to allocate to growth and reproduction (Madsen and Shine 2000, Madsen et al. 2006). The overall links between annual rat numbers and python demography were broadly linear.

Mean and minimum body sizes of reproductive female pythons were atypically low in 2010 because of depressed growth rates of these snakes over the three preceding years, due to the flooding event that decimated the dusky rat population. In spite of their small body size, female pythons did not modify clutch sizes relative to maternal body sizes. Instead, their response was to mature at later ages (at four instead of two to three years), but at a smaller body size, and thus produce smaller clutches. Age, not body size, thus appears to be the main factor initiating reproduction, suggesting that some "internal clock" tells the females to initiate reproduction in spite of their small body size. A study that manipulated feeding rates of captive house snakes (Lampropolis fufinogus) reported that food-deprived females grew more slowly and initiated reproduction later and at smaller body sizes than did their well-fed conspecifics, as well producing smaller clutches (Byars et al. 2010). These results support the hypothesis that the relationships we documented in the field population were a result of straightforward links between food intake, growth, and reproductive output.

Despite the simplicity of the relationship between food intake and reproductive output, the curvilinear nature of the reaction norms for female body size at maturation (caused by the exceptionally small body sizes of reproductive females in 2010) would not have been predicted from our earlier data. Thus, our results suggest that in order to robustly predict responses of demographic traits to extreme environmental conditions, we need to study animals across the entire range of parameter values that they may experience. This is no
easy challenge. Climate change models predict an increased frequency of extreme weather events, such as the flood that eradicated the rats from the Fogg Dam floodplain. Similarly extreme weather events are likely to increase in frequency and severity with global warming (Easterling et al. 2000). As evident from our previous 16-year study, even long-term research programs may fail to incorporate such extreme conditions. Laboratory-based studies (e.g., Byar et al. 2010) may be useful in that they enable investigators to expand the range of parameter values (food intake rates) to be tested. However, we doubt that institutional ethics committees would approve the harsh nutritional regimes that water pythons in our study site encountered after the inland tsunami of March 2007; our mark-recapture studies suggest that >55% of the snakes died of starvation over this period (Ujvari et al. 2011).

Ecological theory suggests that reaction norms often will evolve such that organismal responses remain at relatively consistent (optimal?) levels across a wide range of environmental circumstances (Via et al. 1995). For example, food intake rates may be buffered against variation in prey availability by facultative responses such as satiation at higher extremes, and by increased foraging activity or broadened dietary composition at lower extremes (Shine and Madsen 1997). Indeed, water pythons showed a significant broadening of their diet during the three years of low rat abundance, mainly consuming squamate prey (Ujvari et al. 2011). Similarly, energy reserves may be held relatively constant, over a wide range of feeding rates, by a flexible allocation of nutrients among competing pathways (maintenance vs. storage vs. growth vs. reproduction; Kearney et al. 2010). However, in support of the findings by Ghalambor et al. (2007), our analyses suggest that selection to linearize reaction norms will be intense only over the range of typically encountered conditions. By definition, extreme events occur so infrequently that they are unlikely to impose effective selection on adaptively tuned responses. Thus, organisms may show unpredictable responses when the usually encountered range of conditions is exceeded. That uncertainty reinforces the need for long-term field studies if we are to predict the ways in which natural populations will respond to future changes in global climate.

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