CLIMATIC DETERMINANTS OF THE REPRODUCTIVE TIMING IN THE ASIAN HOUSE GECKO, *HEMIDACTYLUS FRENATUS* DUMÉRIL AND BIBRON (GEKKONIDAE)

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ABSTRACT. — Small ectotherms are strongly affected by their immediate environment and so respond sensitively to climate. The climatic determinants of reproductive timing in a reptile species may, ultimately, determine the geographic range of that species, and these determinants are, thus, of particular interest when the species is invasive. Here we examine climatic correlates of reproductive timing in the invasive asian house gecko, *Hemidactylus frenatus*, across two sites representing its long-established and recently-introduced range. We collected data on the proportion of gravid females in Darwin, Australia (its introduced range) over two years, and compared that with previously published data from the gecko's long-established range (in Bandung, Java, Indonesia). Our analysis suggests strong site differences in the response of this species' reproductive timing to climate. In both sites, high minimum monthly temperatures were strongly associated with increased numbers of gravid females, but the effects of other variables (maximum temperature and moisture availability) were more site dependent. These site differences may be due to many factors, including plasticity, and evolution, which we are unable to elucidate here. The differences between sites in the response to climatic variables, however, suggests it may be difficult to determine the climatic limits to this species' range based on a simple analysis of climate.

KEY WORDS. — *Hemidactylus frenatus*, reproductive timing, introduced species, invasive species

INTRODUCTION

Predicting the final distribution of an invasive species is a complex problem (Phillips et al., 2008). A useful first step in developing predictions of a species' final range is to understand how climate affects various critical aspects of the species' life history (e.g., Kearney & Porter, 2004). In studying this problem, small ectotherms make ideal research foci, because small-size and ectothermy increase the impact of climatic variables on the organism. Thus, diurnal and seasonal fluctuations in temperature, for example, will closely determine when and where an ectotherm can be active. When the small ectotherm in question is also an invasive species, the research is of immediate relevance to predicting eventual distribution limits.

The Asian house gecko *Hemidactylus frenatus* is amongst the most widespread gecko species in the world. From putative natural origins in tropical Asia (Case et al., 1994), the species has colonised many areas in the Pacific, tropical Americas and Africa (for details see Hoskin, 2011), and continues to expand, with new distributional records regularly appearing in the literature (e.g., Jadin et al., 2009; Hollis, 2006; Paredes-Leon & Reynoso, 2006). In Australia it has been present since at least 1841 (Fisher & Calaby, 2009), but until recently has been restricted to a few small areas in the north (McKay et al., 2009). The ubiquitous and conspicuous presence of this species has facilitated much research into aspects of its biology, most notably its invasion ecology (e.g., Petren et al., 1993; Cole et al., 2005), but also other aspects of its biology, such as diet (e.g., Petren & Case, 1996; Galina-Tessaro et al., 1999) and reproduction (e.g., Church, 1962; Murphy-Walker & Haley, 1996; Ota, 1994). Rödder et al (2008) predict the potential range of *H. frenatus*, using climate niche data derived from voucher locations, to cover much of the tropics.

Like most geckos, *H. frenatus* typically lays two hard-shelled eggs, which are normally deposited in a dry, hidden place such as beneath bark or in the cracks of window frames. As

with most ectotherms, the survival of gecko eggs is highly dependent on the environment; in general low temperatures cause long incubation times with decreased survival, and dessicating conditions will quickly kill the eggs. In *H. frenatus*, the eggs require a gestation period of between 46–80 days depending on temperature (Chou, 1979; Brown & Reyes, 1956; Ota, 1994), and eggs incubated below 19°C do not survive (Ota, 1994). Because eggs are so sensitive to temperature and humidity, the timing of parturition in reptiles is under strong optimising selection; females are only likely to lay eggs at times and in places where those eggs have a good chance of survival (Brown & Shine, 2006). Thus, by examining the timing of parturition and its climatic correlates, we can explore which climatic factors are critical for reproduction in *H. frenatus*. Given that reproduction is a critical aspect of any animal's life-history, the climatic correlates of reproductive timing may well be eventual climatic limits on the species' range. Here we investigate the climatic correlates of reproductive timing in *H. frenatus* at two sites encompassing both its long-established and recently-introduced range. We examine the climatic correlates of reproductive timing as well as how these correlates vary between sites.

METHODS

Estimating the timing of reproduction in Darwin. — Darwin is situated on the northern Australian coast within the wet-dry tropical climate zone, and experiences a dry season from May–Sep with average temperatures between 19–30°C. Eighty percent of rainfall occurs during the wet season (Oct–Mar), when temperatures are higher, averaging between 25–33°C (Bureau of Meteorology, Darwin). For the period of Mar.2005 to Jan.2006 one of us (JLM) conducted visual surveys of *H. frenatus* at 32 sites in suburban Darwin, recording the total number of *H. frenatus*, and the number which showed the presence of eggs in the later stages of development in the lower abdomen. Surveys were conducted in the first few hours after sunset, as this is a time of high activity (Frankenberg & Werner, 1981). Each site comprised one or more buildings, and ranged in a spectrum of artificial light regimes from constant (ie schools and shops) to ambient. In each calendar month up to 12 sites were surveyed, by slowly patrolling an established circuit of surfaces suitable for gecko activity and inspecting any geckos with a hand-held light. In this way, we collected data on 1175 geckos. Although visual in situ assessment of reproductive condition is less accurate than dissecting specimens for that purpose, it has the advantage that sampling is non-destructive, and is both time and effort-efficient. Eggs are clearly visible when the animals are in a paler mood of their colour spectrum, and typically appear as a pair of offset, pale-coloured, slightly ovoid shapes in the posterior torso. They may be distinguished from the occasional white matter visible in the viscera by their shape and by their position close to the lateral margin of the body. Any animal that did not display large obvious eggs of at least 8×7 mm was scored as not gravid. Because this method may underestimate the actual number of gravid animals, our results are biased towards lower detection thresholds. Animals estimated visually to be immature (smaller than 37 mm snout-vent), or which did not present a pale transluscent dorsal colouration (which allows eggs to be visible) were excluded from the counts.

We pooled the numbers across sites from each month, as there were no demonstrable differences per site. To assess the effect of climate on the proportion of gravid geckos, we used climate data for the same time period from the closest weather station (Darwin Airport; Bureau of Meteorology), providing data on monthly mean maximum and minimum temperature, total monthly rainfall, and mean monthly relative humidity at 1500 h.

Comparing reproduction and climate patterns from other locations. — Church (1962) collected data on reproductive timing in *H. frenatus* from Bandung, central Java (within the species' long-established range). Because Church's data were collected in a similar way to ours, and because he reported climatic records for Bandung during the period of his surveys, we were able to explicitly compare his data with ours. Church's dataset contains records on 923 animals collected over a 12-month period, and is thus also similar in size and duration to our own. His study site, the city of Bandung, is situated at 768 m asl and experiences a tropical climate with depressed seasonal variation. The wet season extends from Nov–Mar, when 70% of the year's precipitation falls and temperatures average 19–27°C. Remaining dry season months average 18–28°C (Indonesian Bureau of statistics).

Others have investigated the seasonality of egg-production in *H. frenatus* (Ota, 1994; Murphy-Walker & Haley, 1996; Ramirez-Bautista et al., 2006) but none of these data were directly comparable to ours (either because animals were raised in captivity, or percentage of gravid animals was reported with males excluded). Hence we confine ourselves to a qualitative comparison between our data and theirs (see DISCUSSION).

Statistical treatment. — We used a multiple logistic regression to examine the effect of climatic variables on the proportion of females that were gravid in both Bandung and Darwin populations of *H. frenatus*. We examined the influence of location (Darwin or Bandung), and four climatic variables (monthly mean maximum temperature, monthly mean minimum temperature, monthly mean relative humidity at 1500 h, and monthly total precipitation). These climatic variables are likely to be important to *H. frenatus* because it is a small ectotherm (for which temperature is thus a critical factor) and they lay water permeable eggs (which will dessicate without sufficient moisture and drown if moisture is in excess).

In multiple regression analyses, collinearity between explanatory variables may result in poor parameter estimation (Quinn & Keough, 2002) so before our analysis we examined correlations between explanatory variables. In our dataset, correlations were generally low ($r < 0.5$) in all cases except between rainfall and relative humidity variables ($r = 0.74$). Thus, we used the first principal component of rainfall and

humidity as a single "moisture" variable; eigenvectors of this PC indicated strong positive weights on precipitation and relative humidity. In addition to this transformation, we standardised (mean = 0, s.d. = 1) all variables to assist model convergence and ease the interpretation of interaction terms (Jaccard & Turrisi, 2003).

We conducted logistic regression analysis in a model-selection framework using Akaike's Information Criterion (AIC) as a measure of model performance (Burnham & Anderson, 2002). Under this criterion models within 2 AIC units of the best model have substantial support, models between 2–7 units of the best model have some support and models greater than ten AIC units from the best model have essentially no support. Because we had no a priori expectation as to the best model describing our system, we used all combinations of explanatory variables to create models for assessment. To make analysis and model interpretation tractable, however, we only explored second order interactions in each possible model, and only the best combination of interaction terms (as judged by improvement in AIC value) was used for each combination of variables.

RESULTS

Reproduction in Darwin, Australia. — In 2005, gravid females were present in March, October, and November. At the beginning of the study period, in March, there was a low proportion of gravid females: less than 5%, which reduced to zero in the next month and remained so until October, when the proportion reached an abrupt peak of 12.5% before decreasing by more than half in November (Fig.1a).

In 2006–2007 gravid females were present from Jan–Jun (excluding February) and also from Oct.2006 – Jan.2007 (Fig. 1b). The number of months in which gravid females were

detected differed greatly between the two periods, with 3 of 8 surveyed months in 2005, and 9 of 13 surveyed months during 2006–2007. However in both periods the proportion of gravid females was greatest in Apr, Nov, and Jan. Hence breeding occurred at all times of the year except the late dry season, and was at its greatest rate during the pre-rainy and rainy seasons.

Reproduction in Bandung, Java. — From the data by Church (1962), in Bandung for the year of 1960, gravid females (females with eggs in oviducts) were present in every month. The months of Feb–Oct show gravid females comprising
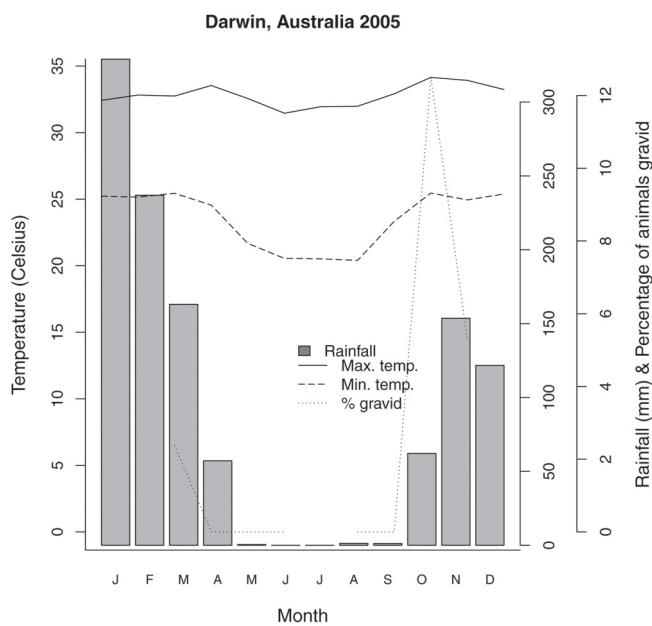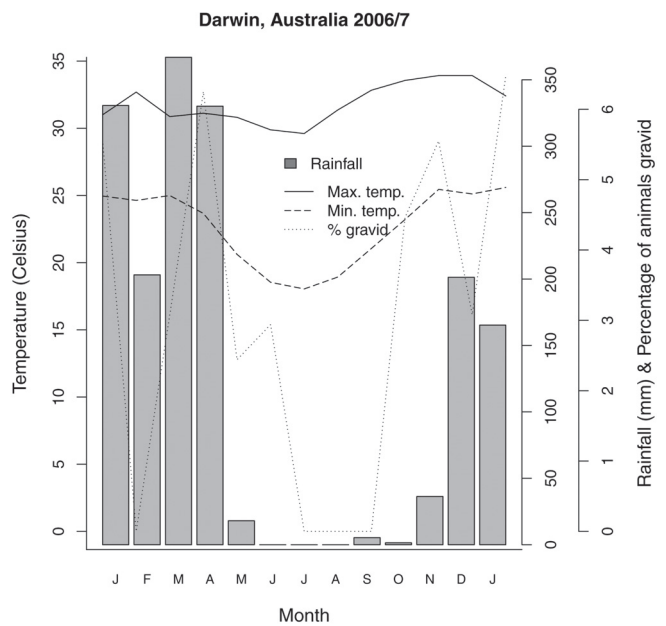

Fig. 1b. Monthly proportion of gravid *Hemidactylus frenatus* and climate variables for Darwin, Australia, in 2006/7 (13th month is January 2007).

Fig. 1a. Monthly proportion of gravid *Hemidactylus frenatus* and climate variables for Darwin, Australia, in 2005.
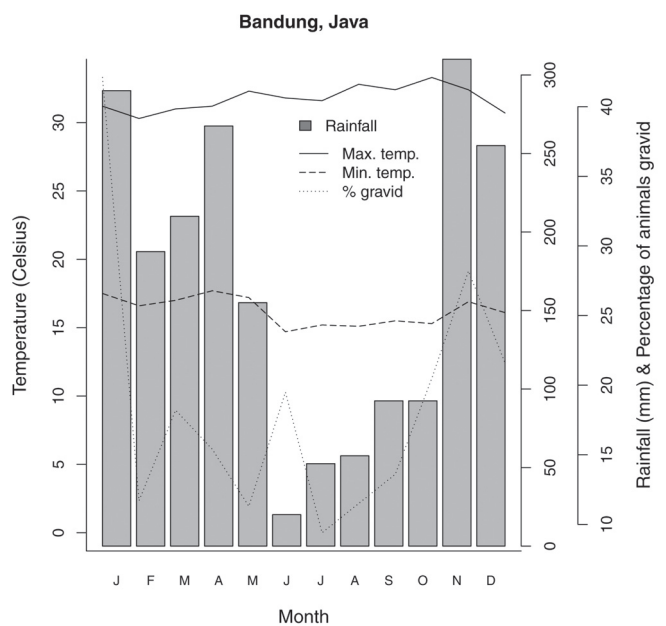

Fig. 1c. Monthly proportion of gravid *Hemidactylus frenatus* and climate variables for Bandung, Java, in 1960. (Data from Church, 1962).

between approximately 10–20% of the population, with the lowest being 9.4% of the sample (n= 52) in August. Percentage of animals with eggs increased from Nov–Jan, reaching a peak in January of 42.1% (n= 19) (Fig. 1c).

Correlates of female reproductive activity. — Model selection identified a best model in the candidate set and only one other model was within 2 units of this best model (Table 1). The best model contained all predictor variables and three interaction terms (between location and each of the climatic variables) indicating that all climatic variables appear to have an influence on reproductive timing of female *H. frenatus*, but that the effect of the environmental variables differed between localities. Parameter estimates for each of the factors indicated that the probability of encountering gravid females was higher in Bandung than Darwin, was higher when minimum temperatures were high (irrespective of locality interactions), was lower when maximum temperature was high (irrespective of locality), and was lower at high moisture levels in Darwin, but higher at high moisture levels in Bandung. Interaction terms tended to reinforce temperature effects (with temperature effects being stronger in Darwin in both cases), but reversed the effect of moisture (such that the effect of moisture was negative in Darwin but positive in Bandung).

The second best model in the candidate set was much simpler and only included location (probability of encountering a gravid female being higher in Bandung) and minimum temperature (probability of encountering a gravid female being higher at high minimum temperatures). Indeed, the predictor weights for each variable (a measure of the relative importance of each variable) confirmed that both location and minimum temperature were the most important variables influencing the probability of encountering a gravid female (weights >0.93 in both cases). Moisture and maximum temperature, on the other hand, were less so (weights < 0.69).

DISCUSSION

Our data show some influence of climate on reproductive timing in *Hemidactylus frenatus*. In Darwin, *H. frenatus* breeds mostly in the pre-rainy and rainy seasons, but may breed at other times of the year, excepting the late dry, a time of year which is well known for depressed activity in reptiles of the Australian wet-dry tropics (e.g., Christian et al., 1995, 1996, 1999). A similar pattern applies to Bandung, Java, except that breeding here does not cease. Analyses of the climatic factors influencing these patterns at both sites suggest that minimum monthly temperature was the most consistent climatic factor in both locations, with a greater chance of encountering gravid females when minimum temperatures were high. Maximum temperature also appeared to have a weak effect on house gecko reproduction (with geckos being less likely to be gravid at high maximum temperatures). Lastly, moisture appeared to have some effect on reproduction in *H. frenatus*, but this effect was both weak and variable in influence, depending on the locality. Overall, climatic factors

only explained around 5% of variation in the probability of encountering a gravid female (Table 1).

The strongest pattern in our data was the clear influence of minimum monthly temperature on the timing of gecko reproduction. This effect is intuitively sensible, because *H. frenatus* eggs take much longer to incubate at low temperatures (increasing their exposure to pathogens and predators) and will die if incubated at a constant low temperature, so females should choose to lay eggs at the warmest time of year (as judged by minimum temperature). This result is supported by analyses from other localities, (Hawaii, Taiwan, and Japan) where breeding in *H. frenatus* takes place in the warmer months (Murphy-Walker & Haley, 1996; Cheng & Lin, 1977; Ota, 1994). While the onset of reproduction may depend upon rising minimum temperatures, however, it is likely that temperature thresholds for egg production vary from site to site. In our dataset, there are indications of interactions between each of the climate variables and location, suggesting that while house geckos do respond to climate, they do so in locality-dependent ways. Thus it is difficult to predict the effect of climate on the reproductive timing of house geckos in a new locality: while we can suggest that the onset of egg-laying may be timed to coincide with increasing temperatures, the exact temperature at which egg-laying will commence is likely to vary between localities.

These site-specific climate effects could be driven by several scenarios. First, we have compared a long-established population with a newly-established one. Successful new or introduced populations are often (through founder effects, evolution or serial introductions) different in numerous traits when compared with older or native-range populations (Kolbe et al., 2007; Simons, 2003). Thus, the Darwin population may have different climatic thresholds for breeding than the Bandung population. Second, *H. frenatus* may display high plasticity for reproductive timing such that individuals spend their growth phase acclimating to their environment. If this is so, then each population of *H. frenatus* will have subtly differing responses to climate. In this case, the limits to this plasticity will need to be understood before climatic factors can be used to infer range-limits through reproductive timing. Third, the constraints on reproduction between the two populations may differ simply because of the differing environments (independent of variation between the populations). For example, extreme high temperatures in Darwin may limit reproduction in this locality at the hottest times, whereas maximum temperature is not as severely limiting in Bandung. Thus Bandung populations respond strongly to water availability, whereas Darwin populations must respond to seasonal fluctuations in temperature before anything else. Last, these locality dependent effects may be the result of evolution at each locality. Because reproductive timing is of crucial importance to small ectotherms, natural selection will rapidly optimise reproductive timing to the climatic conditions peculiar to each locality. These selective forces could create rapid divergence in the cues associated with reproductive timing, particularly in the absence of continued gene flow from a founding population, as often

Table 1. Ranked models exploring the effect of climatic variables and location on the probability of observing a gravid female *Hemidacylus frenatus*. Numbers in the factor columns represent partial regression coefficients for log odds of non-gravid/gravid. Models are ranked by AIC distance from the best model (Delta AIC). w_i is the model weight, and the predictor weights indicate the relative support for each factor in the model.

				Factor		R^2	K	-LL	AIC	Delta AIC	w_i
Loc (Darwin - Bandung)	Max temp	Min temp	Moisture PC		Interactions						
0.577	0.154	-0.416	-0.186		Loc*Max 0.387 Loc *Min -2.279 Loc*PC 0.774	0.063	8	461.87	939.74	0.00	0.51
1.584	-	-1.042	-		-	0.051	3	467.72	941.44	1.70	0.22
1.615	-0.078	-1.037	-		-	0.051	4	467.50	943.01	3.27	0.10
1.666	-	-1.105	0.031		-	0.051	4	467.70	943.39	3.65	0.08
0.510	-0.382	-	-0.323		Max*PC 0.228	0.052	5	467.03	944.06	4.32	0.06
-	-0.293	0.281	-0.446		Min*PC 0.246	0.050	5	468.05	946.09	6.35	0.02
-	-	0.173	-0.341		0.297	0.045	4	470.45	948.91	9.17	0.01
0.390	-	-	-0.265		-	0.042	3	471.79	949.59	9.85	0.00
0.597	-0.130	-	-		-0.203	0.039	4	473.50	954.99	15.25	0.00
0.537	-	-	-		-	0.034	2	475.81	955.63	15.89	0.00
-	-0.173	-	-0.481		-	0.030	3	477.77	961.54	21.80	0.00
-	-	-	-0.408		-	0.028	2	478.92	961.83	22.09	0.00
-	-	0.328	-		-	0.014	2	485.64	975.28	35.54	0.00
-	-0.108	0.369	-		-	0.015	3	485.14	976.27	36.53	0.00
-	-	-	-		-	0.000	1	492.67	987.33	47.59	0.00
-	-	-	-		-	0.001	2	492.38	988.75	49.01	0.00
Predictor Weights											
0.973	0.690	0.937	0.682		0.070						

happens during species introduction. Further research will be necessary to discriminate between these possibilities.

Overall, our data suggest that the timing of reproduction in female *H. frenatus* is complex. Likely climatic factors in a linear model account for only around 5% of the variation in the probability of observing a gravid female, and the way in which these factors influence reproductive timing appears to vary between locations. Such a result heralds caution with regard to using climatic factors and simple relationships to predict the timing of reproduction (and hence the duration of the breeding season) in *H. frenatus* throughout its introduced range. Nonetheless, the apparent divergence between localities in reproductive cues warrants further attention with regard to plasticity of responses and the potential rapid evolution of reproductive timing.

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