Do gravid females of oviparous gekkonid lizards maintain elevated body temperatures? *Hemidactylus frenatus* and *Lepidodactylus lugubris* on Oahu

Yehudah L. Werner

Department of Zoology, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel

Since the discovery that reptiles behaviorally maintain specific body temperatures (BT) (Herter, 1940; Cowles and Bogert, 1944; Huey, 1982; Avery, 1982), attention to intraspecific variations in thermoregulation has gradually increased. Shine (1980) has reviewed 24 studies in which sex and reproductive state were examined as a source of variation in oviparous or viviparous squamates. In all studies (n = 17) of viviparous species, thermoregulation of females or gravid females differed (in either direction) from that of males or other females. In a field study of the common live-bearing gecko of New Zealand, *Hoplodactylus maculatus*, the females (presumably mostly gravid) had higher BT than males (Werner and Whitaker, 1978). This tendency is shared by *Gerrhonotus coeruleus* (Stewart, 1984) and presumably by those squamates in which gravid females bask more than other individuals (Shine, 1980). The higher BT accelerates the development of the young (Blanchard and Blanchard, 1940; Petzold, 1982; Werner, 1986), shortening the exposure of the mother to increased risk of predation due to her hampered locomotion (Shine, 1980; Beuchat, 1986; Brodie, 1989).

From assorted data in Petzold (1982), raising the incubation temperature by 10°C would reduce the incubation period by 48.2% on average (Q₁₀ =2). Moreover, *Pituophis melanoleucus* embryos suffered fewer anomalies developing at 24-32°C than at 21-23°C (Burger et al., 1987).
Hypothetically, any ecological pressure to elevate BT in gravid females could operate also in oviparous species. But there is no evidence that oviparous females, even when ovigerous, differ in their BT (Fitch, 1956; Schall, 1977; Shine, 1980). In a preliminary field study of the gecko * Ptyodactylus hasselquistii guttatus*, BT was insignificantly higher in males than in females (Werner and Goldblatt, 1978). The lack of conclusive results from oviparous species may reflect the difficulty in ascertaining gravidity and the shortness of its period, so that samples of gravid females are diluted with other females or too small.

In the present study I searched for any modification of BT in gravid females of oviparous geckos. Small Gekkoninae are suitable because their large, calcareous-shelled eggs can be identified through their semitransparent abdominal skin. An obvious requisite would be that the study species practices fairly precise thermoregulation, as do some diurno-nocturnal geckos (Werner and Whitaker, 1978; Arad et al., 1989). Hence two such species were investigated during a visit to the Hawaiian island of Oahu: *Hemidactylus frenatus* Duménil and Bibron, 1836 and *Lepidodactylus lugubris* Duménil and Bibron, 1836. The latter is parthenogenetic.

Temperature data obtained for another question (Werner, in press) were reanalysed for the present purpose. Both species are diurno-nocturnal; they thermoregulate in daytime whereas at night they forage, and depending on the habitat, individuals of each may have low BTs (approximating air temperature or BTs resembling daytime BTs (Werner, in press). I obtained deep rectal BTs and concurrent air temperatures of these two gekkonines with a Schultheis thermometer in July 1978. Many females of both species were gravid, and eggs of both species abounded in nature. When an animal was caught, first BT was taken, then sex, gravidity and rostrum-anus length were noted and the animal was released, and air temperature (where the animal had been) was taken. Data were collected day and night, and from various habitats for each species. Some geckos were huddled in groups but mostly, particularly near scattered lights at night, geckos were solitary. The data for each species and sex were initially pooled from all habitats and times, and the sexes compared by t-test. Differences in BT between male and female *Hemidactylus* and between nonpregnant and pregnant *Lepidodactylus* were significant. But as neither the pooling of all subsamples nor the parametric test were justifiable, the data were retested: only those subsamples which had not differed from each other were pooled (Werner, in press). For the samples thus formed, sexes (or states of pregnancy) were compared by the nonparametric 2-sample tests of both Wilcoxon and van der Waerden (Hajek, 1969), and in each case the higher (less favourable) P-value of the two was adopted. Although the results are again not quite conclusive, they are compatible with a hypothesis that the gravid females do maintain somewhat elevated BTs.

The data from 132 animals (tables 1-3) show a consistent trend: females averaged slightly higher BTs than males, and gravid females averaged the highest BT. This held not only for *Hemidactylus* (table 1) and *Lepidodactylus* (table 3) from situations in which they were obviously able to thermoregulate, but even for *Hemidactylus* on trees at night.
Table 1a. Thermoregulating *Hemidactylus frenatus* (from trees in daytime; and from building day or night): body temperature (BT), air temperature (AT), and the difference between them (BT-AT).

<table>
<thead>
<tr>
<th>subsample</th>
<th>n</th>
<th>BT, °C (X SD)</th>
<th>AT, °C (X SD)</th>
<th>BT-AT, °C (X SD)</th>
<th>significance of difference btw. BT &amp; AT</th>
</tr>
</thead>
<tbody>
<tr>
<td>males</td>
<td>45</td>
<td>29.12 ± 2.82</td>
<td>26.41 ± 1.61</td>
<td>2.642 ± 2.52</td>
<td>p = 0.0000</td>
</tr>
<tr>
<td>females</td>
<td>41</td>
<td>29.4 ± 2.38</td>
<td>27.0 ± 1.35</td>
<td>2.43 ± 2.31</td>
<td>0.0000</td>
</tr>
<tr>
<td>nongravid</td>
<td>24</td>
<td>29.3 ± 2.38</td>
<td>26.8 ± 1.24</td>
<td>2.472 ± 2.28</td>
<td>0.0002</td>
</tr>
<tr>
<td>gravid</td>
<td>17</td>
<td>29.62 ± 4.5</td>
<td>27.21 ± 5.0</td>
<td>2.392 ± 4.1</td>
<td>0.0037</td>
</tr>
</tbody>
</table>

Table 1b. Significance of differences between subsamples in table 1a.

<table>
<thead>
<tr>
<th>sample pair</th>
<th>significance of difference in</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BT</td>
</tr>
<tr>
<td>all females vs. males</td>
<td>n.s.</td>
</tr>
<tr>
<td>gravid females vs. males</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

Table 2. Non-thermoregulating *Hemidactylus frenatus* (from trees at night): body temperature (BT), air temperature (AT) and the difference between them (BT-AT).

<table>
<thead>
<tr>
<th>subsample</th>
<th>n</th>
<th>BT, °C (X SD)</th>
<th>AT, °C (X SD)</th>
<th>BT-AT, °C (X SD)</th>
<th>significance of difference btw. BT &amp; AT</th>
</tr>
</thead>
<tbody>
<tr>
<td>males</td>
<td>4</td>
<td>24.90 ± 0.27</td>
<td>24.80 ± 1.6</td>
<td>0.100 ± 0.41</td>
<td>n.s.</td>
</tr>
<tr>
<td>females</td>
<td>5</td>
<td>26.00 ± 0.88</td>
<td>25.30 ± 0.33</td>
<td>0.720 ± 0.41</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

Table 3. Thermoregulating *Lepidodactylus lugubris* (from trees and buildings in daytime): body temperature (BT), air temperature (AT), and the difference between them (BT-AT).

<table>
<thead>
<tr>
<th>subsample</th>
<th>n</th>
<th>BT, °C (X SD)</th>
<th>AT, °C (X SD)</th>
<th>BT-AT, °C (X SD)</th>
<th>significance of difference btw. BT &amp; AT</th>
</tr>
</thead>
<tbody>
<tr>
<td>nonpregnant</td>
<td>14</td>
<td>27.81 ± 1.23</td>
<td>26.60 ± 0.78</td>
<td>1.240 ± 0.99</td>
<td>n.s.</td>
</tr>
<tr>
<td>pregnant</td>
<td>23</td>
<td>28.52 ± 2.20</td>
<td>27.01 ± 1.31</td>
<td>1.511 ± 1.76</td>
<td>0.0091</td>
</tr>
</tbody>
</table>

(202), when BT differed from air temperatures by less than 1°C (Werner, in press: table 1a), a difference that was presumably due to residual heat from the daytime (Werner and Whitaker, 1978). But none of the differences in BT between these samples were significant (0.05 level).

However, females and especially gravid females also exceeded males in the air temperatures at which they were found (tables 1-3). In this case, two of the tests were
significant: in thermoregulating Hemidactylus frenatus (table 1), the air temperature at which gravid females were found exceeded that of males ($P = 0.0540$); and that of all females, that of males ($P = 0.0346$).

The extent to which BT was elevated above air temperature was in all cases (tables 1-3) equal for males, nongravid females and gravid females; i.e., no differences were significant.

These comparisons of BT between gravid (ovigerous) females and other con-specifics, or between females and males, largely excluded potential variation related to geography, habitat, season, time of day or behaviour. In both Hemidactylus ($n = 86+9$) and Lepidodactylus ($n = 37$) the BT of gravid females averaged 0.3-1.1°C higher than in males or nongravid females. Although the differences were insignificant, because of the following circumstances I believe that they do reflect the situation in nature: (1) The differences were in the same direction in the three samples (table 1-3). (2) The direction of the differences was the same as in the viviparous gecko Hoplodactylus maculatus (Werner and Whitaker, 1978). (3) Some of the accompanying differences in air temperature were significant (table 1b) despite the fact that for each subsample they had been recorded from numerous and diversified situations; obviously the gravid females were occupying warmer sites. (4) Most of the geckos were solitary when recorded so their precise locations in the natural thermal gradients probably did not result from social interactions. (5) Within each subsample BT was much more variable (SD) than air temperature; probably some individuals had visited zones of different ambient temperatures, and some of the variation in BT was due to handling.

I tentatively conclude that in the oviparous geckos H. frenatus and L. lugubris the gravid females behaviorally thermoregulate a somewhat higher BT than other individuals.

An elevated BT may improve the fitness of a gravid female gecko in several ways. The temperature tolerance of squamate embryos is almost as wide as that of conspecific adults (Fitch, 1964; Fitch and Fitch, 1967), but temperature has implications for both the mother and her offspring, beyond direct survival. (1) As mentioned above, elevating the incubation temperature accelerates embryonic development and abbreviates the period of increased maternal vulnerability to predation. (2) Although only extreme temperatures kill the embryos, their normal development (size, mensural and meristic characters and gross normalcy) depends on a much narrower temperature range (Burger et al., 1987; Beuchat, 1988). (3) Apparently sex determination in geckos is temperature dependent (Wagner in Bull, 1980; Tokunaga, 1985, 1989). Thus the incubation temperature may be important for assuring a proper sex ratio, though the thermoregulation of mothers may be relevant only in the viviparous species. (4) A sexual or reproductive difference in temperature preference, leading to partial niche segregation, may reduce intraspecific food competition (Mushinsky et al., 1980; Huey, 1982).
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References


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