I studied the effect of incubation environment on loggerhead hatchlings from 14 clutches by comparing the characteristics of hatchlings from eggs at the periphery of clutches (i.e., those in direct contact with the surrounding soil) to the characteristics of hatchlings from eggs in the center of clutches (i.e., those not in direct contact with the surrounding soil). Eggs from the periphery gained more weight (water) during incubation than eggs from the center. Hatchlings from the center eggs were larger in carapace width than hatchlings from the peripheral eggs. Temperatures were monitored throughout the incubation period at various locations within three of the clutches. The center of the clutch was the warmest location and the area most likely to produce female hatchlings. As adults, male loggerheads are able to reproduce twice as often as female loggerheads. To help counter the reproductive advantage of males, female loggerheads might get a reproductive headstart by growing faster and maturing at an earlier age than male loggerheads. If this is the case, then temperature-dependent sex determination is advantageous in loggerheads because it associates female hatchlings with the fastest growth rates.

The adjustment of the $P$ and $S$ parameters for a particular set of incubation temperatures and sex ratio is performed using maximum-likelihood analysis and the

\[
P_i = \frac{C^{n_i}_{m_i} S^{n_i}_{m_i} (1 - S(t_i))^{m_i}}{\sum_{j=1}^{u} P_j} \text{ equation 2}
\]

The likelihood of the experiment ($L$) is then simply:

\[
L = \prod_{i=1}^{u} P_i \text{ equation 3}
\]
variance of the parameters are obtained by the values of the second order derivative at the maximum-likelihood $S$ and $P$ values (Girondot, 1999). The test for significant difference between the observations for each incubation temperature has been established based on the hypothesis number of males and females for each incubation experiment (C.J. Limpus, pers. comm.). The probability of the observed common sex obtained at this temperature (J.D. Miller and D. coriacea), that their phenotype were in fact identical to the most described in this experiment but further studies have shown each of the $\lambda$ experiments ($L_j$) is calculated as well as the likelihood of of the $\lambda$ experiments ($L_j$). The test is then performed using a $\chi^2$ with $2\lambda - 2$ DF:

$$\chi^2 = -2 \ln \left( \frac{L_{c}}{\prod_{j=1}^{\lambda} L_{j}} \right)$$ equation 4

Computer program for MS-DOS and MacOS is freely available on the web page: http://www.biop7.jussieu.fr/perso/girondot.html

Results

The pivotal temperature ($P$) and TRT$_{5\%}$ are shown in Table 1 for the available data in literature about marine turtles. Three species need to be discussed in further detail.

*Chelonia mydas:* Only data from Godfrey (1997) are used for the estimations of $P$ and $S$. Data from Mrosovsky et al. (1984) does not permit to reach some maximum likelihood. It can be easily explained because only 4 incubation temperatures were studied and the two intermediate temperatures produced inverse sex ratio tendency compared to the two extreme temperatures. This could be the result of difference in cooling due to change of substrat for incubation (Mrosovsky, pers. comm.). Miller and Limpus (1980) estimate sex ratio for Australian population of this species at 3 incubation temperatures but none produced mixed sex ratio whereas at least two are required to estimate $P$ and $S$. Nine intersexes were originally described in this experiment but further studies have shown that their phenotype were in fact indentical to the most common sex obtained at this temperature (J.D. Miller and C.J. Limpus, pers. comm.). The probability of the observed number of males and females for each incubation temperature has been established based on the hypothesis that sex determination is the same than for Suriname Green turtles. The probability of the observed number of males and females is $>0.99$, $<0.0001$ and $>0.99$ for incubations at 26, 29 and 33°C respectively. Result at 29°C shows that *C. mydas* from Australia therefore exhibits a significant difference for TSD compared to *C. mydas* from Suriname.

*Dermochelys coriacea:* Binckley et al. (1998) reported sex ratio versus incubation temperatures for Leatherback nesting at Playa Grande, Costa Rica (Pacific). Based on a visual comparison with data from Atlantic (French Guiana) TSD in Leatherbacks (Rimblot et al., 1985; Rimblot-Baly et al., 1986), they conclude that: “The two temperature versus % female curves for Atlantic and Pacific leatherback populations are virtually identical in pivotal temperature and overall shape. A reanalysis of these data has concluded that Atlantic and Pacific pivotal temperatures are indeed not significantly different but that TRT is significantly larger for Leatherbacks from Playa Grande (Pacific) compared to French Guiana (Atlantic) (Chevalier et al., 1999).

*Caretta caretta:* TSD has been studied for 6 different geographic origins of animals and permit to use the likelihood ratio test. A significant global difference for TSD is observed (Fig. 1). This demonstrates a significant genetic structure of populations for this species as already demonstrated with mtDNA polymorphism (Encalada et al., 1998).

Conclusions

The first method that uses all the informations available to describe TSD in reptiles is presented. When applied to available data for marine turtles, this method permits the calculation of pivotal temperature and TRT and also their standard-deviations.

This method can be used also to distinguish populations of *C. caretta*, *C. mydas* and *D. coriacea* based on their sensitiviy to temperature. This new statistical tool will permit us to enhance the ecological and evolutionary work on temperature-dependent sex determination.

Acknowledgments

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References


Chevalier, J., M.H. Godfrey, and M. Girondot. 1999. Significant difference of temperature-dependent sex determination between French

Table 1: Pivotal temperature ($P$) and TRT$_{5\%}$ for marine turtles (SD is standard deviation).

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>$P$ (SD)</th>
<th>TRT$_{5%}$ (SD)</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. mydas</em></td>
<td>Suriname</td>
<td>29.14 (SD 0.18)</td>
<td>3.23 (SD 0.464)</td>
<td>1</td>
</tr>
<tr>
<td><em>L. olivacea</em></td>
<td>World</td>
<td>30.06 (SD 0.24)</td>
<td>3.95 (SD 0.047)</td>
<td>2, 3</td>
</tr>
<tr>
<td><em>C. caretta</em></td>
<td>North-Carolina, USA</td>
<td>29.15 (SD 0.11)</td>
<td>3.24 (SD 0.353)</td>
<td>4</td>
</tr>
<tr>
<td><em>C. caretta</em></td>
<td>Georgia, USA</td>
<td>28.19 (SD 0.17)</td>
<td>4.65 (SD 0.706)</td>
<td>4</td>
</tr>
<tr>
<td><em>C. caretta</em></td>
<td>Florida, USA</td>
<td>29.09 (SD 0.11)</td>
<td>3.18 (SD 0.647)</td>
<td>4</td>
</tr>
<tr>
<td><em>C. caretta</em></td>
<td>Mon Repos, Australia</td>
<td>27.85 (SD 0.22)</td>
<td>5.89 (SD 0.765)</td>
<td>5</td>
</tr>
<tr>
<td><em>C. caretta</em></td>
<td>Heron Island, Australia</td>
<td>28.87 (SD 0.22)</td>
<td>4.59 (SD 0.294)</td>
<td>5</td>
</tr>
<tr>
<td><em>C. caretta</em></td>
<td>Brazil</td>
<td>29.15 (SD 0.06)</td>
<td>1.75 (SD 0.070)</td>
<td>6</td>
</tr>
<tr>
<td><em>E. imbricata</em></td>
<td>Antigua</td>
<td>29.27 (SD 0.04)</td>
<td>0.97 (SD 0.007)</td>
<td>7</td>
</tr>
<tr>
<td><em>D. coriacea</em></td>
<td>Costa Rica, Pacific</td>
<td>29.43 (SD 0.01)</td>
<td>1.17 (SD 0.040)</td>
<td>8</td>
</tr>
</tbody>
</table>

Figure 1: Significant TSD difference between Caretta caretta populations ($\chi^2=107.12, 10$ DF, $p<0.01$). The sex ratios (Y axes) are shown in “male frequency.”


