EXPLORING THE RELATIONSHIP BETWEEN DEGREE-DAYS AND
DATE OF METAMORPHOSIS
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Abstract

The hyperbolic relation between ambient temperature and the
development time of cold blooded animals is postulated to repre-
sent a threshold phenomenon. Rate of development is assumed pro-
portional to temperature excess over maintenance level, and a
transition from one developmental stage to the next (e.g.,
hatching of the egg) then occurs when the accumulated excess
temperature reaches a threshold value. A numerical example
illustrates the application of this model to the time required
for metamorphosis of insects held at controlled temperatures.

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On the assumption that cold blooded animals require ambient temperatures in excess of some basal, maintenance level $b$ in order to develop, and that development then proceeds at an instantaneous rate proportional to this excess, we arrive at the conclusion that the developmental stage $S(t)$ at time $t$ is a function of the integrated excess temperature,

$$S(t) = F\left(\int_0^t [h(x)-b]dx\right) = F(H(t)-bt)$$

where $h(x)$ is the temperature at time $x$. A recognizable stage of development such as that which marks the onset of metamorphosis would then occur at a time $t$ when the function $H(t)-bt$ achieves some threshold value $a$; that is, then

$$H(t) = a + bt.$$

**Controlled temperature experiments.** When developing organisms are reared at constant temperature $T_1$ the integrated temperature at time $t$ is

$$H_1(t) = T_1t = a + bt$$

or

$$t = \frac{a}{T_1-b}.$$
The model thus implies that the time \( t \) at which metamorphosis occurs is hyperbolically related to temperature. Since the time origin also is arbitrarily specified, however, we may expect to find that a more appropriate model is:

\[
t - c = \frac{a}{T_i - b}
\]

or

\[
t = \frac{a}{T_i - b} + c.
\]

Graphing such data for different controlled temperatures we should therefore find:

Numerical example. An insect having an aquatic larval stage was reared to an identifiable developmental point in the fifth instar where it displays specific signs of beginning metamorphosis. Individuals reaching this stage in the laboratory were then held at a reduced temperature to halt further development until a predetermined number (20) were available for a controlled temperature bath. Days to emergence of the adult form were then measured at each of five different constant temperature regimes with 20 organisms per temperature level. The following table presents the temperature levels \( T_i \) and the number of days \( t_i \) to
first emergence (out of 20 emergence times) at each temperature.

<table>
<thead>
<tr>
<th>Temperature</th>
<th>$T_i$</th>
<th>12.5</th>
<th>15</th>
<th>20</th>
<th>25</th>
<th>30</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time (observed)</td>
<td>$t_i$</td>
<td>76</td>
<td>48</td>
<td>25</td>
<td>17</td>
<td>14</td>
</tr>
<tr>
<td>Time (predicted)</td>
<td>$\hat{t}_i$</td>
<td>76.2</td>
<td>45.8</td>
<td>25.4</td>
<td>17.6</td>
<td>13.5</td>
</tr>
</tbody>
</table>

The predicted time was calculated from the formula

$$
\hat{t}_i = \frac{\hat{a}}{T_i - \hat{b}} = \frac{286.4}{T_i - 8.74}
$$

where the constants $\hat{a}$ and $\hat{b}$ were estimated from the data in a somewhat unorthodox manner. Writing

$$
t_i = \frac{a}{T_i - b} \quad \text{as} \quad t_i T_i - bt_i = a
$$

and then taking first differences to eliminate $a$,

$$
t_1 T_1 = t_2 T_2 = b(t_1 - t_2) \quad \text{or} \quad Y_1 = bX_1
$$

$$
t_2 T_2 = t_3 T_3 = b(t_2 - t_1) \quad \text{or} \quad Y_2 = bX_2
$$

$$
\vdots
$$

etc.

then

$$
\hat{b} = \frac{\sum X_i Y_i}{\sum X_i^2} = 8.74^\circ C.
$$

$$
\hat{a} = \frac{1}{k} \sum_{i=1}^{k} t_i (T_i - \hat{b}) = 286.4
$$
Thus, 8.74°C is interpreted as the basal, maintenance level temperature and 286.4 degree days is the minimal accumulated temperature (in excess of 8.74°C) required for emergence. For other numerical illustrations see, for example, H. D. Crofton, "Ecology and biological plasticity of sheep nematodes. I. The effect of temperature on the hatching of eggs of some nematode parasites of sheep". Cornell Veterinarian Vol. 55:242-250, 1965.

Variable temperature. It would also be interesting to study controlled temperature regimes which are not constant:

\[ H(t) = a + bt \]

where, again, we should find

Variation among individual organisms is also a matter of interest in such experiments, and with organisms which pass through several identifiable developmental stages (e.g., instars) it would be interesting to determine \( a \) and \( b \) for each stage. Presumably, the organism would have evolved in a manner to accommodate \( a \) and \( b \) to the changing seasons. At a given developmental stage, individual differences could be studied with a view to identifying major sources of variability among both external and internal factors; for example, do individuals
all tend to have the same b but different a thresholds, or are both a and b relatively constant while individuals differ in their ability to utilize excess heat energy beyond the basal level b?

**Field studies.** Where temperature is monitored under field conditions and records are kept of the number "emerging" each day (or attaining some other identifiable developmental stage) then similar analyses may be performed. Again, it would be of interest to examine variation among individuals, which should be more pronounced than in the controlled experiments.

**Speculation on the model.** If we assume that rate of development is proportional to h(t)-b in the sense that

\[
\frac{S'(t)}{S(t)} = k[h(t)-b]
\]

then

\[
S(t) \sim e^{k[H(t)-bt]} \quad (\text{Q}_{10} \text{ model?})
\]

If we further assume that there is a constant risk of producing a cell which triggers the next developmental stage then the time T to this next developmental stage will follow an exponential probability distribution,

\[
P(T > t) = e^{-e[H(t)-bt]}
\]

with density function

\[
f(t) = e^{h(t)-b]}e^{-e[H(t)-bt]}
\]

A numerical example of this density function is illustrated in the attached graph to show that it does have the ability to resemble field data, and is therefore worth looking into despite its seeming over-simplicity.
\( t = \text{time} \)

\[ \text{Humidity} = \frac{H}{(t)} \]

\[ \text{Temperature} = n(t) \]