‘Time enters as an essential element into our definition of organism.’

Russell, 1930, p. 171

Timing, duration, rate and sequence of developmental stages and processes vary between individuals, strains and closely related species. Such shifts and changes are usually dichotomized as acceleration, where development is advanced, or retardation, where development is slowed. This statement assumes that embryos measure time and not some other metric such as size, and that we possess stable reference points to compare timing of development between different organisms. Obtaining such reference points, even for closely related organisms, is no easy task.

23.1 STABLE REFERENCE POINTS: TIME, SIZE OR RATES

The most commonly used reference points are:

1. measures of maturity, or such major events in ontogeny as morphological stage(s), hatching, birth, attainment of sexual maturity and onset of metamorphosis;
2. measures of growth, such as growth rate, size at a particular time during ontogeny and size at maturity; and
3. measures of chronological age, either absolute age (days, months, years), or such measures of relative age as percentage of time through ontogeny or percentage of final size.¹

Although debate over whether time or size should be the metric of choice in analyses of variation in development and growth has raged for decades, there is still no objective way to decide which criterion or combination of criteria to use. Some, such as relative age, are extremely sensitive to temperature, metabolic rate and body size, and are not necessarily correlated with one another during ontogeny, nor under the same control.

Size is influenced by many factors including temperature, nutrition and litter size. For species with external development, temperature is an especially important environmental variable influencing rate of individual development. Because of additive genetic variation, rates of embryonic development can change rapidly in response to selection. Neyfakh and Hartl (1993) demonstrated a response to artificial selection at elevated temperatures in as little as three generations in *Drosophila*. Catch-up growth (and indeterminate growth in organisms whose final size is not fixed) also influences final size.

Maturity and age are less dependent on factors that influence size, but are certainly not independent of them. Attainment of sexual maturity, times of hatching, birth and termination of growth are all subject to evolutionary change. As reference points all must be used with caution.²
Table 23.1  The periods of avian ontogeny, their duration, the metrics suggested for their quantification, and estimated mass-specific energy metabolism for each period

<table>
<thead>
<tr>
<th>Period</th>
<th>Duration</th>
<th>Metric</th>
<th>Metabolized energy (KJ/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Embryonic</td>
<td>Fertilization to hatching</td>
<td>Incubation time</td>
<td>2 ± 0.8</td>
</tr>
<tr>
<td></td>
<td>11–80 days</td>
<td>Morphological stages</td>
<td></td>
</tr>
<tr>
<td>Postnatal</td>
<td>Hatching to sexual maturity</td>
<td>Growth</td>
<td>20–40</td>
</tr>
<tr>
<td></td>
<td>20 days–years</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>Sexual maturity to death¹</td>
<td>Physiological rates such as mass-specific energy metabolism</td>
<td>2400–4300</td>
</tr>
<tr>
<td></td>
<td>8–120 years</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


¹ Estimating longevity in birds is notoriously difficult and many records are anecdotal. Accurate estimates from recovery of banded wild birds in N. America yield upper limits of 21 years 9 months for the White-winged dove, Zenaida asiatica; 20 years 11 months for the Common grackle, Quiscalus quiscula; and 17 years 5 months for Clark’s nutcracker, Nucifraga columbiana (J. Field. Ornithol. [1983], 54, 123–137, 287–294).

One of the earliest experiments in experimental embryology demonstrated size determination in echinoderms. In 1892, Hans Driesch separated the cells of echinoderm blastulae to produce many small but complete embryos and larvae. The chronology of their development did not differ from their larger siblings. Time, not size, is controlled in species with such regulative development. Conversely, normal, but large, tadpoles develop on time when additional material is added to frog gastrulae.

Another pattern occurs in mice, where deletion of cells at the 2- or 4-cell stages nevertheless produces normally sized mid-gastrula embryos that develop on time. Destruction of as much as 80 percent of a 7-day-old mouse embryo is compensated for in only four to five days. These embryos measure time by cell size, not cell number.

Starck (1993) synthesized an extensive body of literature on the evolution of avian ontogenies, which he divided into the three periods shown in Table 23.1. Duration of these periods varies enormously. As each period is size-dependent, physiological rates rather than chronological time could be used as a time standard when comparing avian ontogenies. Because rates of development vary between embryos, physiological rates are also variable and so not ideal metrics for developmental age. Starck advocated morphological stages, growth, and physiological rates as the most practical metrics for the embryonic, postnatal and adult periods respectively (Table 23.1) and concluded that:

‘... the constancy of time patterns in birds implies that heterochrony is not a mechanism of changing ontogenies... in contrast to other vertebrate groups (e.g., amphibians) where heterochrony... plays an important role in the evolution of ontogenies.’

Starck, 1993, p. 292

The postnatal period in birds lasts from 20 days to several years. It has been suggested that growth be related to the time required to increase body weight from 10 to 50% of final size, but growth independent of final size can also be used. Measuring growth over small time intervals in longitudinal studies reveals surprising patterns that show how important it is to make frequent measurement during this period. Humans display saltatory growth during the postnatal period. Indeed, an astonishing 90 to 95% of human development up to 21 months of age is not accompanied by growth but occurs during