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THE MEANING OF DEVELOPMENTAL TIME: A METRIC FOR COMPARATIVE EMBRYOLOGY

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The evolutionary meaning of "developmental time" in animals is an old—and unsolved—problem. Here, I suggest a solution; I do not claim to prove it. I approach this problem from the perspective that the evolution of a lineage is a sequence of ontogenies (life histories); and to understand morphological change in evolution, one must be able to compare the dynamic morphology of one form with that of another. I also assume no fundamental distinction between development and senescence; as Minot pointed out many years ago, "the condition of old age, is merely the culmination of changes which have been going on from the first stage of the germ" (1908, p. 130).

Historically, the evolutionary relevance of time to embryology has largely been considered under the rubric of heterochrony: "changes in the relative time of appearance and rate of development for characters already present in ancestors" (Gould 1977, p. 2). However, such evolutionary processes as acceleration, retardation, progenesis, and neoteny, which are characterized by particular relations of morphology to the age of the organism (as compared with an ancestor), have almost universally been invoked in relating the morphology of one organ to the morphology of some other organ or of the organism as a whole; time as such has not commonly entered into work on heterochrony (see Emerson 1986 for an exception).

In perhaps the most general treatment of this subject, Alberch et al. (1979) introduced a formalism for describing changes in developmental timing that represents ontogeny as a trajectory $\mathbf{X}(t) = [a(t), \mathbf{S}(t), \boldsymbol{\sigma}(t)]$, where a is age, S is size, and σ is shape (the last two may have more than one dimension); within this descriptive framework, heterochrony then appears as a special subset of all the ways in which one ontogeny might be related to another. In applying their formalism, Alberch et al. (1979, p. 301) explicitly assumed that $da/dt = 1$, thus giving age the same dimensions as time. In several examples they had to use either size or shape as their measure of age because information on absolute age was not available, thereby eliminating one of the independent variables. For at least two reasons,

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however, absolute age (in units of clock time) is not an appropriately independent measure of age even if this information is available.

First, there is a pronounced positive relation between the size of an organism and its time scale; in general, small organisms develop more quickly than closely related large ones (Bonner 1965; Calder 1984). In fact, a species that gets larger evolutionarily may be expected to take longer to develop to a given stage. This assumption depends on one's model of the organism as an evolutionary unit; it is analogous to the assumption for size allometry that the allometric relation between the size of a part and the size of the entire organism is more basic than their relative proportions.

Second, the developmental rate in a given species usually depends profoundly on temperature, the rate at warm temperatures often being 10 or more times that at cool temperatures (Needham 1931; McLaren 1965; Brown 1967, 1975*a*,*b*, 1976; Bachmann 1969; Blaxter 1969; Kuramoto 1975). Fisheries researchers have attempted to nullify this effect by introducing degree-days as a measure of developmental time, but this metric is constant only over comparatively narrow temperature ranges (Blaxter 1969). There is also, of course, lesser rate variation caused by unexplained factors even during development at a given temperature (see discussion in Hamburger and Hamilton 1951). In order to compare developmental timing between species, the size and temperature dependence of developmental rates must be accounted for.

Before returning to these points, I must introduce a fundamental distinction in the notion of time, that between time as *sequence* and time as *duration*. Time considered as sequence deals only with the relations "before," "after," and "simultaneous with," whereas time considered as duration also requires some measure of the *interval* between successive events. Comparative embryology has tended to abstract the continual change of the organism as a sequence of states ("stages"), with the durational relations of development usually considered under the category of growth. Unfortunately, most studies of embryonic and adult growth include only fertilization, hatching or birth, and sexual maturity as comparable points in the life cycle (Brody 1945; Laird et al. 1965, 1968; Laird 1966; Sacher and Staffeldt 1974; Frazer 1977). Most normal tables of development include time as a rough correlate of morphological stages (Hamburger and Hamilton 1951; Yntema 1968; Ballard 1973), but this incorporates duration in only a limited sense; a true appreciation of duration must focus on the rate and tempo of change, and these have been largely neglected in comparative embryology. This neglect may be attributed both to historical and to practical factors.

Historically, the Haeckelian search for ancestral adult stages in the ontogeny of descendants has tended to focus attention on the stages themselves rather than on the underlying continuum. Similarly, the transcendental idea of an archetypal form (see Russell 1916) is essentially static. On the practical side, the size and temperature dependence of developmental rate clearly makes any direct comparison between the developmental timing of different species meaningless.

As far as I am aware, only Dettlaff and Dettlaff (1961; see also Dettlaff 1964, 1986) have recognized this problem as one that might admit of a solution. They

proposed dividing the time to any given stage by the time between the first and second cleavage divisions or by the time between the first division and hatching, and they demonstrated that the dimensionless time to any stage, thus defined, remained reasonably constant under different temperature regimes for each of two species of the sturgeon *Acipenser* and four of the frog *Rana*. This constancy is not perfect, however, and when one recognizes that their proposal is identical with claiming that the Q_{10} (the proportional change with a 10°C rise in temperature) of the duration of a given developmental period is the same for all possible periods, it is not difficult to find data that contradict their hypothesis. Yntema (1968), for example, found that the snapping turtle *Chelydra* has a much higher Q_{10} during early development than close to hatching.

Two theoretical objections to their proposal are important. First, to use their measure requires homologizing two different stages (e.g., first and second cleavages) in the species one is comparing. There is thus no possibility of testing the hypothesis that the "developmental duration" between these stages is the same; it must be assumed a priori. Second, in all fairness, the problem Dettlaff and Dettlaff were considering is somewhat different from the one that I am considering here. Their primary objective was to examine the duration in clock time of various developmental periods; they introduced a relative measure because they realized that any other method is bound to fail. There is, however, another distinction one may make in the notion of time: that between clock, or *extrinsic*, time and the rate of aging, or *intrinsic* time. Extrinsic time is an external characteristic of a system, relating its changes to the vibrations of an assumed perfect harmonic oscillator such as an atom or the motion of the earth around the sun. Intrinsic time expresses the rate of change of an internal characteristic of a system and, as such, is closely connected with the idea of an intrinsic age, expressing how far a system has progressed from a certain point (see the discussion in Rosen 1985). This distinction is especially clear if one considers the effect of changing the temperature in the midst of development: the relative time scale of Dettlaff and Dettlaff breaks down completely in this case because the relation between extrinsic time and the intrinsic age (correlated with a given morphological stage) is no longer even approximately constant.

I am seeking a way to measure this intrinsic age—some metric of developmental time that for any species correlates closely with developmental stage but is general enough to allow comparisons between different species. Such a metric must satisfy seven criteria to be useful in comparative studies. I believe that these criteria are both necessary and sufficient for this purpose. (1) The metric should be independent of morphology. (2) The metric should be independent of size. (3) The metric should depend on only one a priori homologous event (e.g., fertilization, mid-blastula transition). (4) The metric should be unaffected by changes in temperature for any given species. (5) Closely related organisms should undergo homologous events at similar developmental ages, as measured by the metric. (6) The metric should increase monotonically with clock time (in the case of gamete production, and perhaps planarian "rejuvenescence," this may need qualification, but in general one expects animals to get "older" with time). (7) The metric should be defined in a physically measurable way.

THEORETICAL FOUNDATIONS

To ask whether some metric can be found that satisfies the criteria above is essentially the same as asking whether there is some *measurable* quantity that remains invariant under each of the transformations $T_1 \rightarrow T_2$, $S_1 \rightarrow S_2$, $\sigma_1 \rightarrow \sigma_2$, and $\Delta t_1 \rightarrow \Delta t_2$, where T is the temperature at which the organism develops, S is the size at equivalent stages, σ is the shape at equivalent intrinsic ages (whatever that might mean), and Δt is the clock time between equivalent stages. This hypothetical quantity may be called an "age invariant"; if it exists, it can be identified with the intrinsic age. The theory of biological similarity, an extension of the theory of physical similarity that provides the basis for all physical comparative biology (see Stahl 1962, 1963; Rosen 1978 and references therein), is expressly concerned with finding such invariants, which can be represented as dimensionless or dimensional product groups of the variables involved (dimensional analysis). A familiar example of this technique is the characterization of hydrodynamic regimes whose state depends on size, density, viscosity, and the rate of flow by a single parameter, the Reynolds number (Stahl 1962). The problem of developmental time is broadly physical (as opposed to narrowly biological), in that one is concerned with how one life cycle is physically scaled to another; one might thus expect similarity theory to apply. As expressed by Rosen: "to the extent that two natural systems can be compared in terms of age, they must be encoded into a common similarity class of dynamical systems" (1985, p. 273). Unfortunately, using this theory requires that one knows either the laws governing the system or, at least, the variables that are relevant (Johnstone and Thring 1957), neither of which are known for this problem. Nevertheless, it is still possible that an age invariant can be found empirically.

A POSSIBLE METRIC

In the physiological literature there has long existed a concept of a "physiological" or "biological" time distinct from ordinary clock time (Loeb 1908, 1919; Loeb and Northrop 1916, 1917*a*,*b*; Pearl 1928; Carrel 1931; du Noüy 1937; Brody 1945). This concept has most recently and most rigorously been applied to the "allometric" scaling of physiological periods in homeotherms (see McMahon 1980; Lindstedt and Calder 1981). Periods such as heartbeat, gestation time, time to 50% of maximum growth, and maximum life span usually scale as $\Delta t \propto M^{1/4}$, where Δt is the length of the period in clock time and M is adult mass. Because the allometric factor is the same for all these periods, their ratios tend to remain constant across species; from this follows the well-known fact that all mammals have about the same number of heartbeats per lifetime.

Boddington (1978), following up on an idea first proposed by Rubner (1908), combined this $M^{1/4}$ scaling of physiological periods with the well-known $M^{3/4}$ scaling of basal metabolic rate (BMR) ("Kleiber's law"; see Kleiber 1975) to derive a constant that he called the "absolute metabolic scope." This constant is a minimum amount of energy expenditure per lifetime per unit of mass, which is approximately the same for all mammals regardless of adult mass. It is most easily

expressed in terms of mass-specific metabolic rate (msMR = MR/M); thus,

$$\text{life span } (\propto M^{1/4}) \cdot \text{msBMR } (\propto M^{-1/4}) = \text{“absolute metabolic scope”} \ (\propto 1). \quad (1)$$

This constant has the dimensions of energy per unit of mass (energy/[mass · time] · time) and was found by both Rubner (1908) and, working with a much larger data set, Stahl (1962) to be about 190,000 calories per gram of wet weight. The “absolute metabolic scope” at first seems like a good age invariant: it shows no significant dependence on absolute size (Boddington 1978), in accordance with criterion 2, and it also seems that closely related organisms have more-similar “absolute metabolic scopes” than distantly related ones, in accordance with criterion 5. Lindstedt and Calder (1981), for example, demonstrated a profound difference between birds and mammals, and I have found (data from Eisenberg 1981) smaller but still significant differences between marsupial and placental mammals (Student's t-test, $t = 3.5$, df = 26, $P < 0.01$).

In spite of its attractiveness, however, when one tries to use this quantity as a measure of developmental time a problem immediately arises: the “absolute metabolic scope,” as defined above, does not allow for ontogenetic changes in body mass and metabolic rate. In equation (1), one is multiplying msMR at a particular stage (adult) by a time period that includes stages of different masses; there is thus no way to interpret physically the quantity arrived at. This can be seen by rewriting equation (1) in integral form:

$$\text{“absolute metabolic scope”} = \text{msMR}(t_a) \int_{t_0}^{t_d} dt \ , \quad (2)$$

where msMR(t_a) is the mass-specific metabolic rate of an adult, t_0 is fertilization, and t_d is death (for now I ignore the distinction between basal, resting, and active MR's).

Concurrent with the ontogenetic change in mass, however, is an ontogenetic scaling of MR, in rough accordance with Kleiber's law, though this relation is complicated by the higher specific growth rates of young animals (Brody 1945). Because of this, young homeotherms have higher msMR's than do adults of the same species. Assuming that the rate of flow of physiological time is proportional to msMR, it follows that physiological time flows more quickly for younger (smaller) homeotherms of a given species. Therefore, in attempting a physical interpretation of physiological age, the energy metabolized/(mass · time) must be integrated over the time period considered; that is,

$$\text{“specific lifetime metabolism”} = \int_{t_0}^{t_d} \text{msMR}(t)\, dt \ . \quad (3)$$

By thus generalizing to more closely tie the concept of a uniform physiological lifetime to that of the rate of flow of physiological time at any moment in the life history, I have laid the groundwork for a further generalization, which is to define physiological time by the integral

$$\text{physiological time} = \int_{t_\alpha}^{t_\beta} \text{msMR}(t)\, dt \ , \quad (4)$$

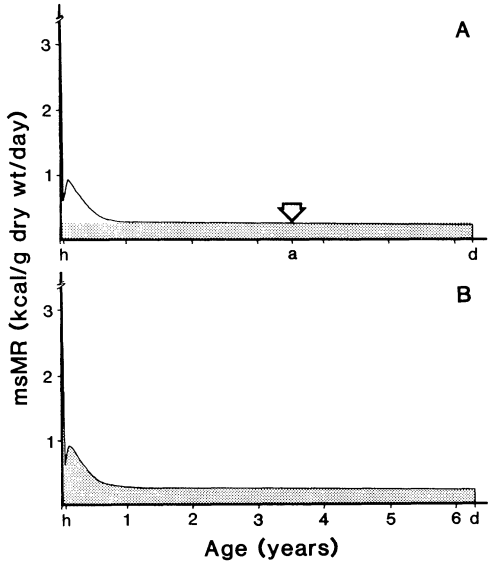

FIG. 1.—Comparison of "absolute metabolic scope" and "specific lifetime metabolism" for *Gallus gallus*. *A*, The shaded area represents the "absolute metabolic scope" (Boddington 1978), as given by equation (2); *B*, the shaded area represents "specific lifetime metabolism," as defined by equation (3). *h*, Hatching; *a*, adulthood; *d*, death. Data from Brody 1945, extrapolated to death.

where t_α is the start of the period under consideration and t_β is the end. I thus give physiological time the dimensions of energy per unit of mass, with the understanding that this is a time-weighted average of the msMR at any given time.

While the jump from equations (3) to (4) is a natural extension of the incorporation of an ontogenetically defined physiological time unit into equation (2), that from equations (2) to (3) involves a mathematical leap away from the supportive data of Boddington (1978), but this is not as unjustifiable as it might first appear. Figure 1 shows the msMR of the chicken (*Gallus gallus*) plotted against time: the shaded area in figure 1*A* represents the integral in equation (2); that in figure 1*B* represents the integral in equation (3). Because the duration of adult life is so much longer than that of the embryo, its high msMR is slightly compensated for by the reduced msMR of old age. More importantly, if the msMR curve is of the same general form for all animals, with high values in the embryo and relatively low, declining values in the adult (one certainly expects this from the increase in size and decrease in specific growth rate; cf. Zotin 1972; Zotin and Zotina 1978), then the difference between equations (2) and (3) is not too great and the approximate invariance of specific lifetime metabolism still holds. I thus propose that physiological time, as defined by equation (4), satisfies the criteria 1–7, above.

With respect to these seven criteria, physiological time is inherently independent of morphology (1), depends on only one a priori homologous event (3), increases monotonically with clock time (6), and is defined in a physically measurable way (7). The three criteria that remain unsatisfied (2, 4, 5) must be evaluated empirically. I have been able to ignore temperature thus far because I have been

dealing only with homeothermic animals; in order to demonstrate that physiological time is independent of temperature (4), I must show that the integral in equation (4), when taken between two equivalent stages of a poikilothermic species developing at different temperatures, remains constant.

Many data (reviews in Needham 1931; Tyler 1939) show that embryos developing at different temperatures require the same amount of energy to reach a given stage, and some demonstrate differences. However, one is concerned not with total metabolism but rather with the integral over time of msMR (a different quantity), and I have found no relevant data on this point. Assuming that organisms of a given species developing at different temperatures have the same mass at equivalent stages and that metabolic rate has the same temperature coefficient as developmental rate (there is some evidence for this; e.g., Tyler 1939), then equation (4) is invariant, and it could be invariant even if these conditions did not hold in a particular case.

Data bearing on the two remaining criteria, size independence (2) and similarity of closely related organisms (5), are examined in the empirical section below. I must first, however, discuss the difficulties in standardizing these data that, at present, prevent definitive testing of the hypothesis.

METHODOLOGICAL CONSIDERATIONS

Mass

In applying the concept of physiological time, one must be able to measure mass-specific metabolic rate in a consistent manner. Both mass and metabolic rate can be difficult to measure, however. Of the two, mass is the more problematic. Not only can hydration state vary, but often there is much extracellular material present: ingested food, bone, horn, hair, and, most important for our purposes, yolk. In almost all invertebrate and vertebrate embryos, the yolk present cannot easily be separated from the embryo itself. This yolk is metabolically inert (Needham 1931; Romanoff 1967) and, if included in the mass estimate, leads to the absurd conclusion that there is no increase in mass during development in these forms. Ideally, one would like some measure of "metabolically active mass" as distinct from this inert material (to use a now-unpopular term, one would like to measure the amount of active protoplasm present).

A reasonable prospect for a measure of this metabolically active mass is the total mass of DNA present, which should obviously correlate quite closely with total cell number. Moreover, the general constancy of the nucleo-cytoplasmic ratio in adults, reflected in the interspecific correlation between cell size and DNA content (Szarski 1976), suggests that this measure would not be affected by differing genome sizes across species. Information on total DNA content is not obtainable for most animals, however. Here I have used only data from animals having meroblastic cleavage, thus allowing the use of mass as the estimate of active protoplasm.

Another question arises with respect to the treatment of extraembryonic membranes, since one would get very different values for mass, especially at early

stages, if these were included. In a general way, though, my proposed measure of physiological time is already an average over the mass of the embryo, since different organs may respire at significantly different rates (Romanoff 1943, 1967), and the question becomes one of whether one wants to examine the whole embryo or just a part of it. Theoretically, this depends on the question one is trying to answer; more realistically, on the data available. Although for most organisms the data on respiration include the entire egg, whereas weight data are for the embryo only, the data sets usually begin late enough that the embryo is quite large relative to extraembryonic structures.

Finally, one must decide whether to use wet or dry weight as the measure of mass. There is no constant relation between these standards; in the chicken, for example, water content rises from 70% early on to about 93% on day 3 and then declines steadily to about 79% at the time of hatching (21 days; Romanoff 1967). This range includes the most typical values for vertebrate embryos (see, e.g., Morris et al. 1983 for *Chelydra*; Smith 1947 for *Salmo*), although D. Vleck et al. (1984) found values of 68% and 64% for hatchling mallee fowl and brush turkeys, respectively. Dry weight seems a more fundamental basis for comparison; for example, Packard et al. (1983), working with the turtle *Chrysemys*, found embryonic dry weight unaffected by hydric conditions of incubation, although both wet weight and carapace length were affected. For data sets in which wet weight was the only information available (see table 1), I have estimated a "dry-weight equivalent" (very roughly) as 15% of the wet weight, using 85% as a typical water content.

Metabolism

By metabolism one generally means heat production in calories, but in adult organisms heat production is proportional to oxygen consumption (1 liter O_2 = 4.8 kcal at standard temperature and pressure; Schmidt-Nielsen 1979); and since this latter quantity is much easier to measure, it is used almost exclusively in physiological research (indirect calorimetry). Some data suggest, however, that this constant relation does not always hold for embryos (see Needham 1931), and ideally, one would use only studies on heat production for calculating physiological times. Unfortunately, most studies of embryonic metabolism have measured O_2 consumption, and I have had to use this as an approximate measure of heat production (for eggs with no external energy source, one can equate heat production with the decline in energy within the egg as measured by bomb calorimetry; see, e.g., Smith 1947).

A more serious problem is the question of how to treat activity versus resting metabolism. The distinction between activity, resting, and basal metabolism (animal fasted, thermoneutral conditions) has been vital for obtaining reproducible results in comparative physiology (Brody 1945). It is important to remember that the "absolute metabolic scope" was defined in terms of basal metabolism; it thus estimates a minimum lifetime energy expenditure. Ever since the work of Rubner (1908) and Pearl (1928), there have been numerous attempts to show that activity shortens the life span by using up the allotted energy more quickly. This work, which has concentrated largely on rats and *Drosophila*, has produced

TABLE 1

PHYSIOLOGICAL TIME UNITS (PTU's) USED FOR DEVELOPMENT

Species	Developmental Time Period, in days*	Range in Embryonic Dry Wt., in mg†	Total PTU's Used, in cal/g of dry wt.‡	Source
Teleostei				
Clupea harengus	3–7 (h)	0.095–0.12	700	Eldridge et al. 1977
	7–12 (f)	0.12–0.085	19,000	Eldridge et al. 1977
Morone saxatilis	1–2 (h)	—	1,900	Eldridge et al. 1982
	2–7 (f)	—	4,900	Eldridge et al. 1982
Salmo gairdneri	22–35 (h)	0.48–1.5	2,500	Smith 1947
	35–83 (f)	1.5–17	8,900	Smith 1947
Chelonia				
Chelydra serpentina	15–55	10–1,220	19,000	Morris et al. 1983 Gettinger et al. 1984
Serpentes				
Aspis cerastes	0–62 (h)	48–930	19,000	Dmi'el 1970
Echis colorata	0–43 (h)	70–910	9,300	Dmi'el 1970
Natrix tesselata	0–37 (h)	26–760	15,000	Dmi'el 1970
Spalerosophis cliffordi	0–60 (h)	30–2,400	19,000	Dmi'el 1970
Vipera xanthina	0–41 (h)	59–1,600	7,800	Dmi'el 1970
Aves				
Agapornis personata	4–22.5 (h)	10–400	20,000	Bucher 1983
Anous stolidus	10–31 (p)	120–2,800	12,000	Pettit & Whittow 1983
	31–35.6 (h)	2,800–3,900	2,700	Pettit & Whittow 1983
Anous tenuirostris	10–29.2 (p)	45–1,800	14,000	Pettit & Whittow 1983
	29.2–34.7 (h)	1,800–2,400	3,600	Pettit & Whittow 1983
Coturnix coturnix	10–18 (h)	270–800	9,300	C. Vleck et al. 1979
Diomedea immutabilis	30–58 (p)	1,500–21,000	12,000	Pettit et al. 1982*a*
Diomedea nigripes	30–58 (p)	1,200–22,000	11,000	Pettit et al. 1982*a*
Gallus gallus	1–4	1–16§	20,000	Romanoff 1967
	4–21 (h)	4.4–6,500	41,000	Romanoff 1967
Gygis alba	12–30 (p)	150–1,500	6,900	Pettit et al. 1981
	30–35.5 (h)	1,500–2,100	5,000	Pettit et al. 1981
Leipoa ocellata	30–62 (h)	500–31,000	29,000	D. Vleck et al. 1984
Pelecanus occidentalis	7–28 (p)	?–7,200	17,000	Bartholomew & Goldstein 1984
Poephila guttata	4–14 (h)	1.5–92	15,000	C. Vleck et al. 1979
Pterodroma hypoleuca	24–42.7 (p)	600–2,900	7,400	Pettit et al. 1982*b*
	42.7–48.7 (h)	2,900–3,400	4,700	Pettit et al. 1982*b*
Puffinus pacificus	13–45 (p)	92–4,900	18,000	Ackerman et al. 1980
	45–50 (h)	4,900–8,800	2,300	Ackerman et al. 1980

* Time to hatching (h), to feeding (f), or to internal or external pipping (p), in days from fertilization for teleosts, from start of incubation for all others.
† Estimated as 15% of wet weight for all except the teleosts, *Chelydra*, *Agapornis*, and *Gallus*.
‡ Estimated from O_2 consumption (1 liter O_2 = 4.8 kcal; Schmidt-Nielsen 1979) except for *Salmo* and *Gallus*.
§ Embryonic membranes included.

equivocal results (see Lints et al. 1984). Most embryos begin moving within the egg, and activity can be quite pronounced during larval stages, even if no feeding occurs. In juvenile and adult animals one can also distinguish heat production associated with the metabolism of food (the "specific dynamic effect" of the food; see Kleiber 1975). This source is present in embryos, but it cannot be dissociated from the basal metabolism. I know of no data relating these factors to developmental rate, although it would be relatively easy to block muscle contraction with an inhibitor and examine the effect on developmental rate and msMR. Here I have assumed that the extra metabolism due to activity can be included with all other metabolism, although I have avoided data on animals that are feeding. Future work will determine to what degree it is necessary to define a "resting" developmental metabolism excluding muscular activity.

RESULTS AND DISCUSSION

As discussed above, two empirical questions need to be examined: is physiological time independent of size? (criterion 2); and do closely related organisms undergo homologous events at similar physiological times? (criterion 5). In the following discussion I refer to the calories per gram of dry weight calculated from equation (4) as physiological time units, or PTU's. Table 1 gives the total PTU's used during the listed periods of embryonic development for all species for which I have been able to find data suitable for analysis. For the reasons given above, the strict comparability of these data between species is questionable. Moreover, in all cases the developmental period considered does not begin at fertilization but rather at a fairly advanced stage, when most organ rudiments have already appeared (the data for the chicken *Gallus* are an exception, beginning much earlier than the rest). Illustrations of developmental stages that can be correlated with the calculated PTU's are available for only five species; the results for all other species must be evaluated on the basis of the percentage of incubation time used. In spite of these confounding factors, I believe that these data strongly suggest that criterion 2 is indeed satisfied, although they cast doubt on the satisfaction of criterion 5. This latter conclusion is rendered less potent, however, by the phylogenetic distance between the species compared.

The most important point to be drawn from an overview of the data as a whole is that, in spite of great differences in the shape of the curves (fig. 2), all the calculated figures in the table are comparable, with a range from 6800 PTU's for the striped bass *Morone* to 61,000 PTU's for *Gallus*, or about an order of magnitude. Considering the roughness of the calculations (due to estimating heat production from oxygen consumption and dry weight from wet weight) and the lack of comparability between the taxa and developmental periods considered, this is a reasonable agreement.

To examine more specifically the effect of mass on the metric, it is best to look at the data for birds, which cover a range from 0.09 g of dry weight at hatching in the zebra finch (*Poephila*) to 31 g of dry weight at hatching in the mallee fowl (*Leipoa*). The three species with the smallest hatching weight—the zebra finch, lovebird (*Agapornis*), and European quail (*Coturnix*)—take about 15,000, 20,000,

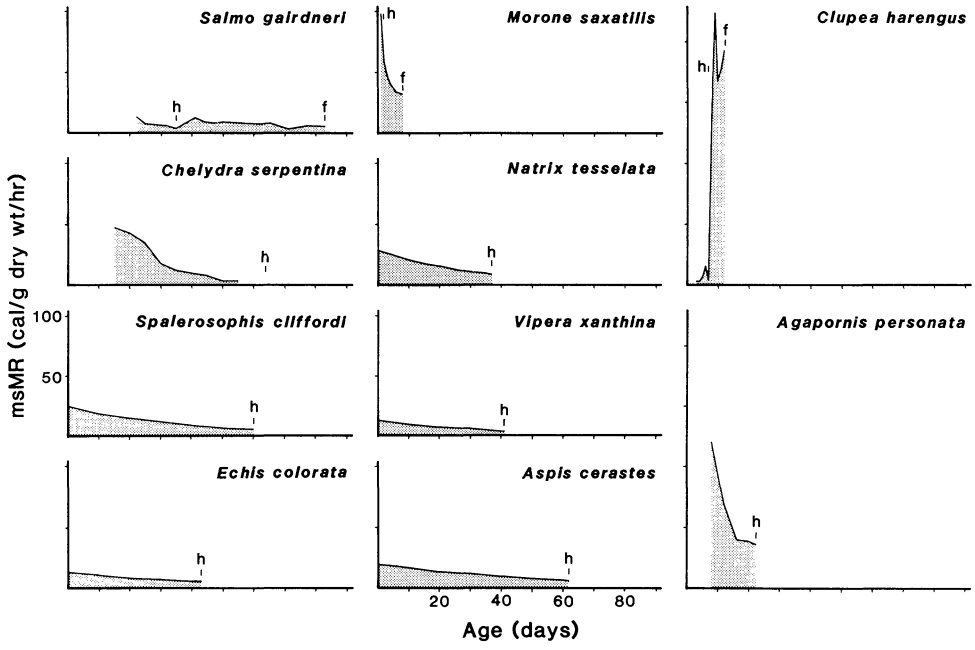

FIG. 2 (*above and facing page*).—Curves of mass-specific metabolic rate (msMR) for all animals included in this study. The shaded area represents physiological time as defined by equation (4) and calculated in the table. Although the developmental periods covered are not strictly comparable between taxa, species with slower development clearly tend to have lower msMR's, thus decreasing the disparity in the area under the curve between species. For more information on individual species, see the table. *h*, Hatching; *f*, feeding; *ep*, external pipping; *ip*, internal pipping.

and 9,300 PTU's for the last 71%, 82%, and 41% of their incubation periods, respectively. The three species with the greatest hatching weight—the mallee fowl, Laysan albatross (*Diomedea immutabilis*), and black-footed albatross (*D. nigripes*)—take about 29,000, 12,000, and 11,000 PTU's for the last 52%, 48%, and 48% of their incubation periods, respectively. The considerable overlap between these groups belies a major effect of mass on the physiological time scale.

To examine the effect of phylogeny, two approaches are possible. First, one can compare morphological development between species directly; this is, of course, the primary use for a metric such as this. As mentioned above, illustrations that can be correlated with physiological time data are available for only five distantly related species. These illustrations are plotted against physiological time in figure 3. For the three teleost species, two major developmental periods should be considered: fertilization to hatching (egg) and hatching to the start of feeding (yolk sac). It is worth noting that the herring takes the least PTU's to hatching but the most to yolk absorption, reflecting the extremely large increase in metabolic rate at hatching in this species (fig. 2). This suggests possible confounding effects of increased activity at this time. Ignoring this potential problem, morphological

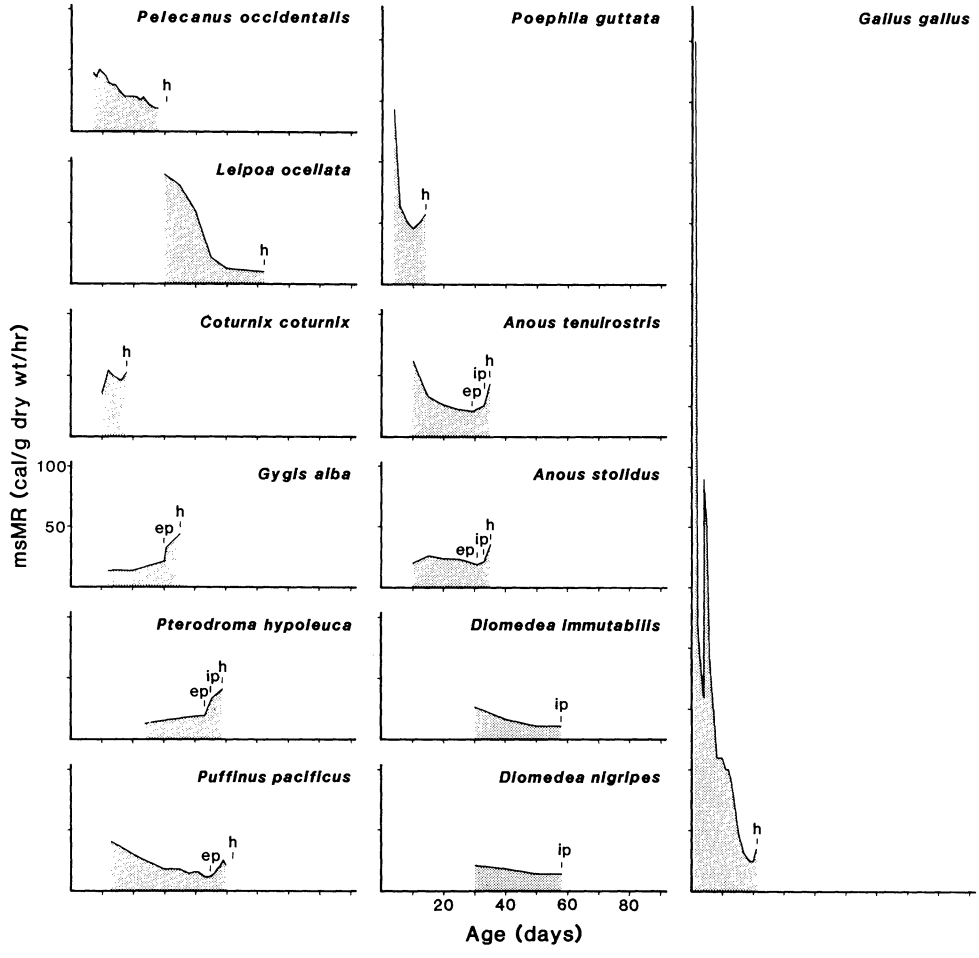

FIG. 2 (*continued*).

change and PTU's correlate here no better than within half an order of magnitude between species.

Comparing these fishes with amniotes indicates that they probably take fewer PTU's from fertilization to hatching than do turtles, snakes, or birds (see the table). However, if one examines the morphology of hatchlings in *Chelydra* and *Gallus* (fig. 3), the two other species for which morphological information is available, it is apparent that the fishes are less developed at hatching and that the start of feeding is a more appropriate stage for comparison. Using this standard, the herring is roughly comparable to amniotes, whereas both the striped bass and trout take fewer PTU's to yolk absorption. The beginning of the physiological data for *Chelydra* appears to be at a later stage than that for *Gallus* (fig. 3); nevertheless, it is apparent that the chicken takes more PTU's to develop from a comparable stage through hatching than does the turtle.

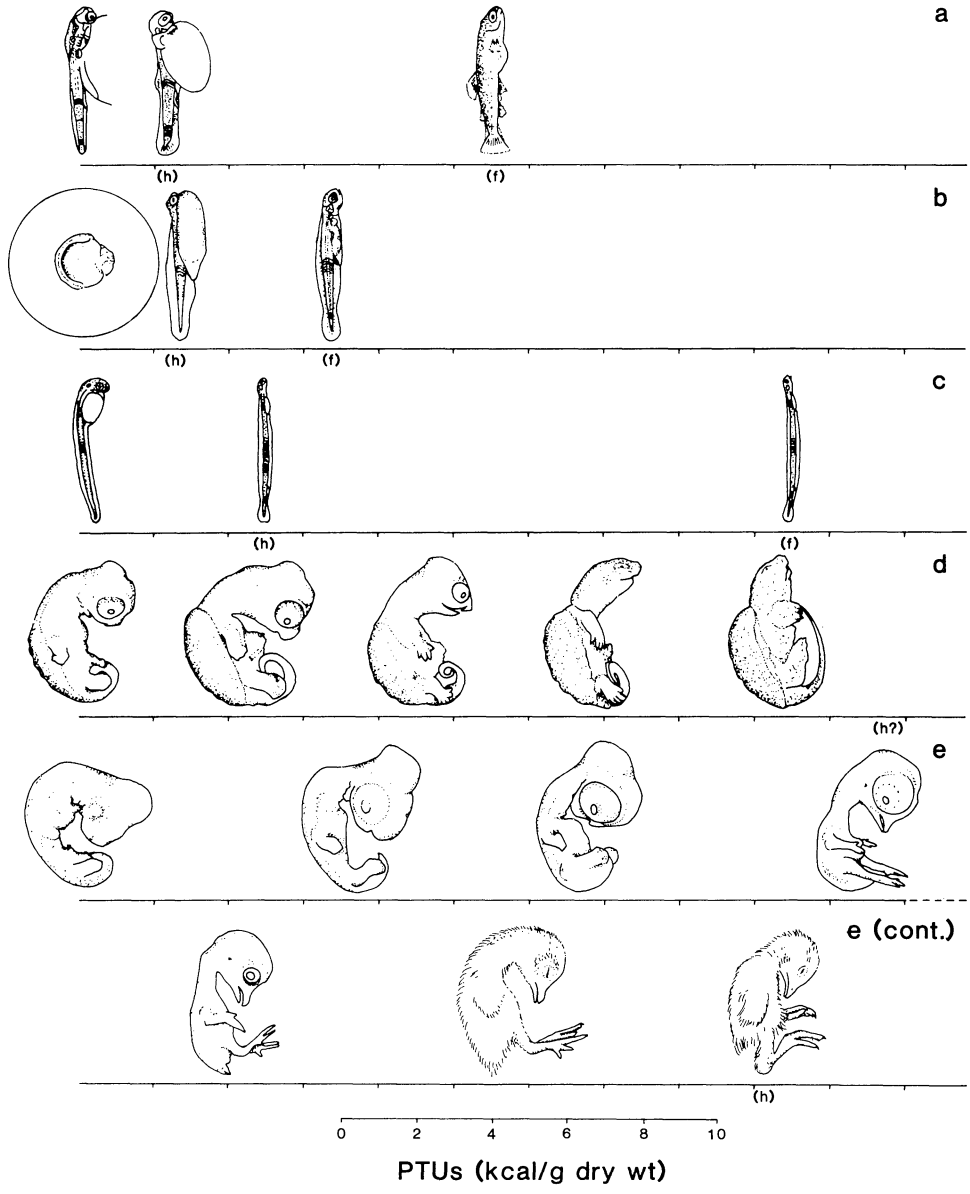

FIG. 3.—Morphological development versus physiological time units (PTU's) for five species: *a*, *Salmo gairdneri* (after Knight 1963; Ballard 1973); *b*, *Morone saxatilis* (after U.S. Fish and Wildlife Service 1978); *c*, *Clupea harengus* (after U.S. Fish and Wildlife Service 1978); *d*, *Chelydra serpentina* (after Yntema 1968); *e*, *Gallus gallus* (after Hamburger and Hamilton 1951). *h*, Hatching; *f*, feeding. Some figures reversed for ease of comparison.

Perhaps the most strictly comparable data on avian development are available in the paper on developmental energetics of *Pelecanus* by Bartholomew and Goldstein (1984), who staged their embryos using the Hamburger and Hamilton (1951) table for the chicken; these data are also the least supportive of the hypothesis. Although the period of data overlap is short, it is clear that, between stages 22 and 25, *Gallus* used about 8,200 PTU's and *Pelecanus* about 1,100 PTU's; from stage 25 to 30, *Gallus* used about 13,000 PTU's and *Pelecanus* about 3,300 PTU's.

As a second approach to examining phylogenetic effects, one can compare the PTU figures for congeneric species. These data are available in two cases. The albatrosses *Diomedea immutabilis* and *D. nigripes* take 12,000 and 11,000 PTU's, respectively, for the last 48% of their incubation periods. The terns *Anous tenuirostris* and *A. stolidus* take 18,000 and 15,000 PTU's for the last 71% and 72% of their incubation periods, respectively. The general agreement seen between congeneric species is in accord with criterion 2, although one might have hoped that the figures for the terns would be closer. It is worth noting that the albatrosses do not lie outside the range of other birds in terms of PTU's, although they, along with other procellariforms (including *Pterodroma* and *Puffinus*), have incubation times and energy costs of incubation per gram of hatchling that are greater than predicted by the allometric equation for all birds (Ackerman et al. 1980; Pettit et al. 1982*a*,*b*).

My proposed use of physiological time as a metric for comparative embryology is thus most strongly supported by the generally comparable PTU figures calculated for all species and especially by the apparent size independence of these figures. It is most weakly supported (or most strongly contradicted) by the scattered data on morphological development. Additional, more-rigorous tests of the hypothesis should be possible when more data become available on developmental energetics as correlated with growth and morphological development. Especially important will be data allowing comparison between closely related species and between embryos of the same species developing at different temperatures.

PROSPECTS FOR THE FUTURE

Increasing attention is being paid in evolutionary biology to the view, long championed by Bonner (e.g., 1965), that the organism *is* the life cycle. From this point of view it is clear that time, on the scale of the individual life cycle, is an—perhaps the—essential dimension for the description of organisms. In the introduction I try to show the inadequacies of ordinary clock time as a metric for this dimension. The most important point has been stressed in almost all previous discussions of physiological or biological time: the rate of flow of intrinsic time varies widely among animals. The implications of this point were suggested more than 50 years ago by Carrel, who perceived that because "living organisms are immersed in the physical universe, their duration must either be placed in the frame of physical time or be used as a frame for physical time. In fact, physical time is referred to physiological duration." (1931, p. 621.)

The introduction of a metric for developmental time satisfying the criteria above would obviously be of the greatest importance, giving substance to concepts that in the past have been largely qualitative and thus all too easily neglected. Already, the "allometric" scaling of physiological time in homeotherms has been used to gain important insights in ecology and life-history theory (Blueweiss et al. 1978; McNab 1980; Lindstedt and Calder 1981). Perhaps the most important effect of such a metric, however, would be to allow a closer connection between life-history theory and the theory of morphological evolution. In this context, I show how a metric would allow one to address two particular issues that have been raised in the past; undoubtedly, new issues and insights will arise if a metric indeed becomes available.

Length of Development

In the nineteenth century one possible argument against the Haeckelian doctrine of ontogenetic evolution by terminal addition of characters was the unreasonable lengthening of development that would result. To counter this, recapitulationists introduced the notion of a "condensation" of ancestral ontogenies such that they would occupy a smaller proportion of development. This was conceived of by Haeckel as a deletion of intermediate stages, such that "ontogeny strikes out on an ever straighter course" (Haeckel 1866; quoted in Gould 1977, p. 84). Cope and Hyatt, in contrast, preferred the "acceleration" of characters into earlier developmental stages by some unknown mechanism, so that, as characterized by Gould, "the stages of ancestral ontogenies are repeated in successively shorter intervals, leaving time for the addition of newly acquired characters" (1977, p. 86). Müller and other Darwinists tried to find a selective basis for condensation, arguing, for example, that "in general it will be useful for an animal to express as early as possible those advantages by which it sustains itself in the struggle for existence" (1915; quoted in Gould 1977, p. 101).

Common to all these viewpoints is the assumption that the time available for development is limited, although it is not clear from the review by Gould what the various parties to the debate really meant by "time." Gould himself did not clearly dissociate time and size, stating that "embryonic stages usually occur much earlier in time and at much smaller sizes than the ancestral adult stage they represent" (1977, p. 74). Seemingly implicit in Haeckel's concept of deletion is a notion that time is proportional to the number of stages an organism passes through, whereas the acceleration of Cope and Hyatt implies a concept of time that is perhaps more closely related to the relative proportion of the entire life history used. It is in fact likely that all the above authors meant all of these things, to some degree or another, by "time" and that these meanings are mixed in with an intuitive notion of intrinsic time, which I have discussed above. It is certainly clear that none of them meant ordinary clock time.

This controversy over the mechanism of condensation died down with the realization that a strict dogma of terminal addition is untenable. One might still ask; however, whether the length of development has increased through phylogeny in "progressive" lineages (those tending toward greater complexity) or has decreased in "retrogressive" lineages. For example, one might see a general trend

in the data presented above for taking more physiological time units for development through hatching along the series from fish to fowl. Such a trend would be compatible with a theory of ontogenetic evolution by terminal addition of characters, with only limited condensation of these characters into early stages (assuming that modern fishes and reptiles are not as "progressive" as birds). Similarly, one might ask whether those directly developing frogs that recapitulate most tadpole features within the egg require more intrinsic time to reach a particular stage than those that do not recapitulate many tadpole features (e.g., *Gastrotheca orophylax* vs. *G. walkeri*; see Wassersug and Duellman 1984).

Length of development has also been an issue in considering the evolution of anuran metamorphosis. Wassersug and Hoff (1982) tried to show that advanced tadpoles undergo a more rapid metamorphosis than primitive ones, in accordance with Williams' (1966) prediction that organisms should hurry through vulnerable periods of their life cycle. They were unable to do more than indicate the probability of this hypothesis, however, owing to the lack of an appropriate time scale: their morphologically based criteria for metamorphic rate were necessarily too dependent on those very changes they were attempting to study.

Truncation versus Retardation

In the formalism of Alberch et al. (1979), a distinction is made between the evolutionary adoption of larval morphology due to a truncation of development (progenesis) and that due to a retardation of developmental rate (neoteny), a distinction also made by de Beer (1958) and Gould (1977). From the work of these authors one sees that it is impossible to distinguish these two modes of evolutionary transformation in practice without the additional assumption of an approximately constant relation between size and (intrinsic) age in the group of species one is comparing. This assumption is probably justified in comparisons between closely related species in groups with little overall size variation, especially when the presumed progenetic species is near the lower size limit for the group as a whole. In fact, size is in most cases a better estimator of the intrinsic age than is absolute age, which as we have seen is subject to many uncontrollable influences. Moreover, it is frequently difficult to determine the absolute age of animals (much less the intrinsic age), especially when one is working with museum specimens or animals obtained from the wild. In these cases it is reasonable to use size as an estimator of age, although it is necessary to be clear that this is what one is doing. It is preferable to leave age out of the analysis altogether and merely state, for example, that "species A matures at a smaller size than species B, and its adult morphology resembles the juveniles of that species."

With a metric for developmental time, the operational distinction between progenesis and neoteny becomes possible. One could determine, for example, whether altricial birds truly hatch at a younger intrinsic age than do precocial birds. In fact, as stressed above, any attempt to describe quantitatively the morphology of an organism as a process in time requires such a metric. Without it, one can only attempt to infer the processes of evolutionary change in developmental timing from data on morphology and size.

SUMMARY

The lack of a suitable metric for developmental time has prevented a comparison of developmental rates and tempos between species, thus precluding analyses of heterochronic processes in evolution that do not depend on the use of morphology or size as an index of age. At least two problems exist in using clock time itself as the measure of developmental time: temperature effects within a species, and size effects across species. Consideration of two important distinctions that can be made in the notion of time—that between time as sequence and time as duration and that between extrinsic and intrinsic time—suggests that a metric, to be useful, must satisfy seven criteria: (1) it should be independent of morphology; (2) it should be independent of size; (3) it should depend on only one a priori homologous event; (4) it should be unaffected by changes in temperature for any given species; (5) closely related organisms should undergo homologous events at similar developmental ages as measured by the metric; (6) it should increase monotonically with clock time; and (7) it should be defined in a physically measurable way.

I propose that physiological time, here defined as the integral of mass-specific metabolic rate over clock time, may be such a metric; this definition is based on an extension of previous concepts of physiological time to reflect ontogenetic changes in mass and metabolic rate. The proposed metric inherently satisfies criteria 1, 3, 6, and 7; satisfaction of the others must be assessed empirically. In spite of problems with strict comparability, literature data from 22 vertebrate species strongly suggest that criterion 2 is also satisfied, although they cast doubt on the satisfaction of criterion 5. No available data bear directly on criterion 4, although circumstantial evidence suggests that it may also be satisfied.

A more rigorous assessment of the hypothesis awaits additional data, especially those allowing a correlation between physiological time and morphological development. However, even if this particular proposal for a metric proves unworkable—which is likely, given its simple formulation and broad scope—the criteria suggested will serve to judge any future proposal of a metric for developmental time. For the present, one must at least be aware of the hidden assumptions that have entered into much previous work on heterochrony, particularly that of an equivalence between size and age. Without a metric for developmental time, the extent and meaning of evolutionary changes in developmental timing simply cannot be assessed.

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LITERATURE CITED

Ackerman, R. A., G. C. Whittow, C. V. Paganelli, and T. N. Pettit. 1980. Oxygen consumption, gas exchange, and growth of embryonic wedge-tailed shearwaters (*Puffinus pacificus chlororhyncus*). Physiol. Zool. 53:210–221.

Alberch, P., S. J. Gould, G. F. Oster, and D. B. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–317.

Bachmann, K. 1969. Temperature adaptations of amphibian embryos. Am. Nat. 103:115–130.

Ballard, W. W. 1973. Normal embryonic stages for salmonid fishes, based on *Salmo gairdneri* Richardson and *Salvelinus fontinalis* (Mitchill). J. Exp. Zool. 184:7–26.

Bartholomew, B. A., and D. L. Goldstein. 1984. The energetics of development in a very large altricial bird, the brown pelican. Pages 347–357 *in* R. S. Seymour, ed. Respiration and metabolism of embryonic vertebrates. Junk, Dordrecht, The Netherlands.

Blaxter, J. H. S. 1969. Development: eggs and larvae. Pages 177–252 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. III. Academic Press, New York.

Blueweiss, L., H. Fox, F. Kudzma, D. Nakashimi, R. Peters, and S. Sams. 1978. Relationships between body size and some life history parameters. Oecologia (Berl.) 37:257–272.

Boddington, M. J. 1978. An absolute metabolic scope for activity. J. Theor. Biol. 75:443–449.

Bonner, J. T. 1965. Size and cycle. Princeton University Press, Princeton, N.J.

Brody, S. 1945. Bioenergetics and growth. Hafner, New York.

Brown, H. A. 1967. Embryonic temperature adaptations and genetic compatibility in two allopatric populations of the spadefoot toad, *Scaphiopus hammondi*. Evolution 21:742–761.

———. 1975*a*. Temperature and development of the tailed frog, *Ascaphus truei*. Comp. Biochem. Physiol. A, Comp. Physiol. 50:397–405.

———. 1975*b*. Embryonic temperature adaptations of the Pacific treefrog, *Hyla regilla*. Comp. Biochem. Physiol. A, Comp. Physiol. 51:863–873.

———. 1976. The time-temperature relation of embryonic development in the northwestern salamander, *Ambystoma gracile*. Can. J. Zool. 54:552–558.

Bucher, T. L. 1983. Parrot eggs, embryos, and nestlings: patterns and energetics of growth and development. Physiol. Zool. 56:465–483.

Calder, W. A., III. 1984. Size, function, and life history. Harvard University Press, Cambridge, Mass.

Carrel, A. 1931. Physiological time. Science (Wash., D.C.) 74:618–621.

de Beer, G. 1958. Embryos and ancestors. Clarendon, Oxford.

Dettlaff, T. A. 1964. Cell divisions, duration of interkinetic states and differentiation in early stages of embryonic development. Adv. Morphog. 3:323–362.

———. 1986. The rate of development in poikilothermic animals calculated in astronomical and relative time units. J. Therm. Biol. 11:1–7.

Dettlaff, T. A., and A. A. Dettlaff. 1961. On relative dimensionless characteristics of the development duration in embryology. Arch. Biol. 72:1–16.

Dmi'el, R. 1970. Growth and metabolism in snake embryos. J. Embryol. Exp. Morphol. 23:761–772.

du Noüy, P. L. 1937. Biological time. Macmillan, New York.

Eisenberg, J. F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. University of Chicago Press, Chicago.

Eldridge, M. B., T. Echeverria, and J. A. Whipple. 1977. Energetics of Pacific herring (*Clupea harengus pallasi*) embryos and larvae exposed to low concentrations of benzene, a monoaromatic component of crude oil. Trans. Am. Fish. Soc. 106:452–461.

Eldridge, M. B., J. A. Whipple, and M. J. Bowers. 1982. Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 80:461–474.

Emerson, S. B. 1986. Heterochrony and frogs: the relationships of a life history trait to a morphological form. Am. Nat. 127:167–183.

Frazer, J. F. D. 1977. Growth of young vertebrates in the egg or uterus. J. Zool. (Lond.) 183:189–201.
Gettinger, R. D., G. L. Paukstis, and W. H. N. Gutzke. 1984. Influence of hydric environment on oxygen consumption by embryonic turtles *Chelydra serpentina* and *Trionyx spiniferus*. Physiol. Zool. 57:468–473.
Gould, S. J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, Mass.
Haeckel, E. 1866. Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie. 2 vols. Reimer, Berlin.
Hamburger, V., and H. L. Hamilton. 1951. A series of normal stages in the development of the chick embryo. J. Morphol. 88:49–92.
Johnstone, R. E., and M. W. Thring. 1957. Pilot plants, models, and scale-up methods in chemical engineering. McGraw-Hill, New York.
Kleiber, M. 1975. The fire of life. Krieger, Huntington, N.Y.
Knight, A. E. 1963. The embryonic and larval development of the rainbow trout. Trans. Am. Fish. Soc. 92:344–355.
Kuramoto, M. 1975. Embryonic temperature adaptation in development rate of frogs. Physiol. Zool. 48:360–366.
Laird, A. K. 1966. Dynamics of embryonic growth. Growth 30:263–275.
Laird, A. K., S. A. Tyler, and A. D. Barton. 1965. Dynamics of normal growth. Growth 29:233–248.
Laird, A. K., A. D. Barton, and S. A. Tyler. 1968. Growth and time: an interpretation of allometry. Growth 32:347–354.
Lindstedt, S. L., and W. A. Calder III. 1981. Body size, physiological time, and longevity of homeothermic animals. Q. Rev. Biol. 56:1–16.
Lints, F. A., E. Le Bourg, and C. V. Lints. 1984. Spontaneous locomotor activity and life span: a test of the rate of living theory in *Drosophila melanogaster*. Gerontology 30:376–387.
Loeb, J. 1908. Über den Temperaturkoeffizienten für die Lebensdauer kaltblütiger Thiere und über die Ursache des natürlichen Todes. Pflügers Arch. Gesamte Physiol. Menschen Tiere 124: 411–426.
———. 1919. Natural death and the duration of life. Sci. Monthly 9:578–585.
Loeb, J., and J. H. Northrop. 1916. Is there a temperature coefficient for the duration of life? Proc. Natl. Acad. Sci. USA 2:456–457.
———. 1917*a*. What determines the duration of life in Metazoa? Proc. Natl. Acad. Sci. USA 3: 382–386.
———. 1917*b*. On the influence of food and temperature upon the duration of life. J. Biol. Chem. 32:103–121.
McLaren, I. A. 1965. Temperature and frog eggs: a reconsideration of metabolic control. J. Gen. Physiol. 48:1071–1079.
McMahon, T. A. 1980. Scaling physiological time. Lect. Math. Life Sci. 13:131–163.
McNab, B. K. 1980. Food habitats, energetics, and the population biology of mammals. Am. Nat. 116:106–124.
Minot, C. S. 1908. The problem of age, growth, and death: a study of cytomorphosis. Putnam's, New York.
Morris, K. A., G. C. Packard, T. J. Boardman, G. L. Paukstis, and M. J. Packard. 1983. Effect of the hydric environment on growth of embryonic snapping turtles (*Chelydra serpentina*). Herpetologica 39:272–285.
Müller, F. 1915. Für Darwin. Pages 200–263 *in* A. Möller, ed. Fritz Müller: Werke, Briefe und Leben. Fischer, Jena, East Germany. [First published 1864.]
Needham, J. 1931. Chemical embryology. 3 vols. Cambridge University Press, Cambridge.
Packard, G. C., M. J. Packard, T. J. Boardman, K. A. Morris, and R. D. Shuman. 1983. Influence of water exchanges by flexible-shelled eggs of painted turtles *Chrysemys picta* on metabolism and growth of embryos. Physiol. Zool. 56:217–230.
Pearl, R. 1928. The rate of living. Knopf, New York.
Pettit, T. N., and G. C. Whittow. 1983. Embryonic respiration and growth in two species of noddy terns. Physiol. Zool. 56:455–464.

Pettit, T. N., G. S. Grant, G. C. Whittow, H. Rahn, and C. V. Paganelli. 1981. Respiratory gas exchange and growth of white tern embryos. Condor 83:355–361.

———. 1982*a*. Embryonic oxygen consumption and growth of Laysan and black-footed albatross. Am. J. Physiol. 242:R121–R128.

———. 1982*b*. Respiratory gas exchange and growth of Bonin petrel embryos. Physiol. Zool. 55: 162–170.

Romanoff, A. L. 1943. Differentiation in respiratory activity of isolated embryonic tissues. J. Exp. Zool. 93:1–26.

———. 1967. Biochemistry of the avian embryo. Wiley, New York.

Rosen, R. 1978. Fundamentals of measurement and representation of natural systems. North-Holland, New York.

———. 1985. Anticipatory systems: philosophical, mathematical and methodological foundations. Pergamon, Oxford.

Rubner, M. 1908. Das Problem der Lebensdauer und seine Beziehungen zu Wachstum und Ernährung. Oldenbourg, Munich.

Russell, E. S. 1916. Form and function: a contribution to the history of animal morphology. J. Murray, London.

Sacher, G. A., and E. F. Staffeldt. 1974. Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth. Am. Nat. 108:593–615.

Schmidt-Nielsen, K. 1979. Animal physiology: adaptation and environment. 2d ed. Cambridge University Press, Cambridge.

Smith, S. 1947. Studies in the development of the rainbow trout (*Salmo irideus*) I: the heat production and nitrogenous excretion. J. Exp. Biol. 23:357–378.

Stahl, W. R. 1962. Similarity and dimensional methods in biology. Science (Wash., D.C.) 137:205–212.

———. 1963. The analysis of biological similarity. Adv. Biol. Med. Phys. 9:355–464.

Szarski, H. 1976. Cell size and nuclear DNA content in vertebrates. Int. Rev. Cytol. 44:93–111.

Tyler, A. 1939. The energetics of embryonic differentiation. Hermann, Paris.

U.S. Fish and Wildlife Service. 1978. Development of the fishes of the Mid-Atlantic Bight: an atlas of egg, larval, and juvenile stages. U.S. Fish Wildl. Serv. FWS-OBS 78/12. Fort Collins, Colo.

Vleck, C. M., D. F. Hoyt, and D. Vleck. 1979. Metabolism of avian embryos: patterns in altricial and precocial birds. Physiol. Zool. 52:363–377.

Vleck, D., C. M. Vleck, and R. S. Seymour. 1984. Energetics of embryonic development in the megapode birds, mallee fowl *Leipoa ocellata* and brush turkey *Alectura lathami*. Physiol. Zool. 57:444–456.

Wassersug, R. J., and W. E. Duellman. 1984. Oral structures and their development in egg-brooding hylid frog embryos and larvae: evolutionary and ecological implications. J. Morphol. 182: 1–37.

Wassersug, R. J., and K. Hoff. 1982. Developmental changes in the orientation of the anuran jaw suspension: a preliminary exploration into the evolution of anuran metamorphosis. Evol. Biol. 15:223–246.

Williams, G. C. 1966. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton, N.J.

Yntema, C. L. 1968. A series of stages in the embryonic development of *Chelydra serpentina*. J. Morphol. 125:219–252.

Zotin, A. I. 1972. Thermodynamic aspects of developmental biology. Monogr. Dev. Biol. 5:1–159.

Zotin, A. I., and R. S. Zotina. 1978. Experimental basis for qualitative phenomenological theory of development. Pages 61–84 *in* I. Lamprecht and A. I. Zotin, eds. Thermodynamics of biological processes. De Gruyter, Berlin.