An integrative approach to heterochrony: the distinction between interspecific and intraspecific phenomena

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While a framework and terminology for heterochrony has been referenced widely in the literature and appears to be accepted by nearly all workers in the field we have found it to be a confusing and incomplete model that has led to varying degrees of misunderstanding about heterochrony among evolutionary biologists. Much of the confusion exists because the model is explicitly limited to phylogenetic patterns (interspecific comparisons), but has been used for intraspecific comparisons. Because heterochrony may underlie all morphological variation and possibly is the developmental phenomenon producing all morphological change it is important that descriptions of heterochronic patterns and processes be clear and precise over all levels of analysis. To this end we discuss and clarify the previous model for heterochrony, reject some of the terminology and suggest alternatives, and then expand the model to include a new nomenclature for intraspecific heterochronic phenomena. Our modifications are essential to maintain the critical conceptual distinction between inter- vs. intraspecific heterochronic patterns and processes in evolutionary biology.

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INTRODUCTION

In the last 20 years, the study of heterochrony — changes in the timing and/or rates of processes underlying the ontogenetic formation of morphological traits — has become one of the focal concepts forging the integration of many areas of evolutionary biology. Several major reviews and papers have set the foundation for the recent increase in empirical studies of heterochrony. Gould (1977, 1992) described the basic modes of heterochrony as perturbations of onset times, offset times, and rates. Alberch et al. (1979) simplified Gould’s (1977) classification, describing heterochronic processes and distinguishing between paedomorphosis (Garstang, 1922) which results in traits produced by truncated development, and peramorphosis which results in traits produced by extended development. Fink (1982, 1988) reformulated the model and emphasized the necessity of phylogenies to polarize directions of heterochronic change between species. The concept has been reviewed from several perspectives including general overviews (McKinney, 1988a; McKinney & MacNamara, 1991), systematics (Kluge & Strauss, 1985; Mabee, 1993), allometry; (McKinney, 1988b; McKinney & MacNamara, 1991; Godfrey & Sutherland, 1995), palaeontology (MacNamara, 1988), quantitative genetics (Atchley, 1987; Slatkin, 1987; Atchley & Hall, 1991), and developmental biology (Alberch, 1982; Bonner, 1982; Hall, 1984, 1990; 1992; Raff & Raff, 1987; Raff & Wray, 1989).

The framework and terminology of the model of Alberch et al. (1979) has been referred to widely in the literature and appears to be accepted by nearly all workers in the field. In spite of this, we have found it to be a confusing and incomplete model that has led to varying degrees of misunderstanding about heterochrony among evolutionary biologists. Confusion exists in four major areas:

(1) Terms have been used inconsistently (cf. neoteny and progenesis).
(2) Terminal shape has been defined in a way that fails to separate somatic from reproductive ontogenies.
(3) Pattern and process have been confused.
(4) The model is explicitly limited to phylogenetic patterns (interspecific comparisons), but has been used for intraspecific comparisons.

Because heterochrony may underlie all morphological variation and possibly is the developmental phenomenon producing all morphological change (De Beer, 1940; Gould, 1977, MacNamara, 1988, Hall, 1992) it is important that our description of heterochronic patterns and processes be clear and precise over all levels of analysis. We will attempt to clarify the model of Alberch et al. (1979: hereafter referred to as the Alberch et al. Model). In doing so, we will define 'terminal shape', reject some of their terminology and suggest alternatives, and then expand the model to include intraspecific phenomena by presenting a new nomenclature for what Reilly (1994) termed intraspecific heterochrony.
We start by reviewing the six simple developmental perturbations that categorize heterochronic change. To clarify our discussion we must review some basic assumptions. First, heterochrony involves the development of traits and does not pertain to whole organisms any more than homology pertains to whole organisms or lineages. There is a real difference between the statements ‘this organism is paedomorphic’ and ‘this organism has a number of paedomorphic characters’, just as there is a real difference between the statements ‘this is a paedomorphic lineage’ and ‘this lineage is characterized by the evolution of a number of paedomorphic traits’. Fink (1982:261) states, “Terming whole organisms paedo- or peramorphic, as a linguistic shortcut, may obfuscate the real complexity of morphogenetic processes.” We assume that the statement ‘this species is paedomorphic’ actually means ‘this species has some number of paedomorphic traits’. Second, we will assume that we have an accurate measurement or descriptor of the trait or shape under study.

Third, we assume that some relevant measure of time obtains. Heterochronic patterns cannot be classified without information or convincing inferences on the actual timing (age) of developmental events in the ancestral and descendant ontogenies (Emerson, 1986; Gould, 1988; Jones, 1988; McInnery, 1988b; Carlson, 1991; Klingenberg & Spence, 1993; Godfrey & Sutherland, 1995). One cannot describe relative onsets, offsets, or rates of development without estimates of the time axis. In many cases, size must be used as a proxy for age. This should be done only when size can be empirically shown to be a good proxy for age, that is, if the relationship between size and age can be shown to be a one to one function. However, the use of size as a proxy for age is widely regarded as problematic or inappropriate (Shea, 1983, 1988; Blackstone, 1987a, b; McInnery, 1988; McInnery & McNamara, 1991; Godfrey & Sutherland, 1995; Klingenberg & Spence, 1993).

Fourth, we describe an ontogenetic trajectory as the development of a trait from its inception to its offset shape (previously called the ‘terminal shape’). We define the ‘offset shape’ for an ontogenetic trajectory as the offset point of the development of a given trait regardless of when it occurs in ontogeny. The timing of this offset point is indicated by any beginning of any asymptote in the ontogenetic trajectory when the rate of change of the trait goes to zero for a period of time. The beginning of a static period (or level portion) of the ontogenetic trajectory marks the end of a certain portion of development for a given trait regardless of when it occurs within the overall ontogeny of the whole organism. The asymptote serves as the offset point for the preceding portion of morphogenesis. The offset shape can be the ‘final’ or ‘terminal’ shape attained in ontogeny or any ‘transient’ shape attained during ontogeny as long as it can be identified by an asymptote in shape development. Thus, depending on your level of analysis, this could involve the entire ontogeny of the trait or any subportion of ontogeny of the trait as it develops. Accordingly, the onset point for the development of a given trait can be described as the beginning of ontogeny or the beginning of any period of shape change during ontogeny. Because ‘shape’ is an inherently multidimensional phenomenon the shape trait used on the shape axis has to be chosen as one or a combination of many dimensions in this space and the choice of the shape trait becomes a crucial part of the analysis because different traits may produce contradictory results in comparisons of the same species (see the sea urchin example discussed on pp.138–140, below).

Fifth, following Fink (1982, 1988), we will assume that a convincing hypothesis of the ancestral ontogeny has been proposed. A phylogenetic hypothesis is essential to polarize patterns in order to identify heterochronic processes (see Bjorklund, 1991,
for a key example). Simple comparison of two ontogenetic trajectories allows us to identify the type of perturbation needed to shift from one to the other (shift in onset, offset, or rate), but simple inspection cannot yield the direction of change. However, when the polarity has been determined (by outgroup comparison), then the direction of heterochronic change in the descendant species is identified. By knowing the type and direction of perturbation one can hypothesize a process of heterochronic change between the ancestral and descendant ontogenies. For example, in going from an ancestral rate to a slower descendant rate, a process of slowing down the rate (deceleration) had to occur. Acceleration/deceleration, hypomorphosis/hypermorphosis, and pre-displacement/post-displacement are processes that result from shifts in rate, offset, or onset. Furthermore, in a more general sense the act of becoming truncated (paedomorphosis), becoming extended (peramorphosis), or being the same by a different trajectory (isomorphosis, introduced below) can be thought of as processes as well, but these terms do not reveal the perturbatory process by which ontogeny was changed (by rate, offset, onset, a combination of these perturbations, or by other developmental mechanisms).

Finally, we assume that heterochrony in somatic traits is being considered independently of heterochrony in reproductive traits. If the timing of sexual maturation is the same in the ancestor and descendant, only somatic shifts are possible. If the timing of maturation and somatic traits are shifted in the descendant then two independent heterochronic phenomena have occurred. Reproductive and somatic trajectories should be plotted and characterized independently and comparisons between them can only be made when actual age axes are available. As we will illustrate below, a major problem with the Alberch et al. Model, is that it unnecessarily links reproductive and somatic development.

THE SIX SIMPLE DEVELOPMENTAL PERTURBATIONS

Alberch et al. (1979) and Fink (1982, 1988) discuss three developmental parameters: rate ($k$), onset time ($\alpha$) and offset time ($\beta$). Perturbations of these parameters can produce a change in ontogenetic timing relative to the ancestral condition (Fig. 1). Our model is operationally similar to the Alberch et al. Model. However, we present a revised set of terms that make clear certain conceptual points not considered by previous authors. For the present discussion, ontogenetic trajectories are drawn simply as straight lines connecting the onset and offset times of development of the trait of interest. In reality ontogenetic trajectories are rarely linear (Godfrey & Sutherland, 1995).

Positive or negative shifts in developmental rate, offset time, or onset time, comprise the six, simple developmental shifts that are possible (Fig. 1). These simple perturbations result in two possible patterns of heterochrony: the ontogeny of some trait in the descendant species can be truncated relative to the ancestral species (paedomorphosis, Fig. 1: y-axis down arrows), or extended relative to the ancestral species (peramorphosis, Fig. 1: y-axis up arrows). The interspecific pattern is deduced by comparing the ontogeny of the descendant species traits to the ontogeny of the ancestral species traits and determining the direction in which the shift occurs. Peramorphosis is produced by an increase in rate (acceleration), a later offset time (hypermorphosis), or an earlier onset time (pre-displacement). Conversely, paedomorphosis is produced by a slower rate (deceleration, new term), an earlier offset
time (hypomorphosis, a term coined by Shea, 1983), or a later onset time (post-
displacement).

Paedomorphosis and peramorphosis can result from multiple perturbations as well, and more often than not heterochrony may involve more than one simple perturbation (Klingenberg & Spence, 1993). Figure 2A illustrates some of this complexity. Note that by mapping ancestor/descendant trajectories in terms of onset time, offset time, and rate, multiple perturbations can be distinguished from simple perturbations as long as the offset shape of the trait of interest has been defined explicitly.

Heterochrony can also occur without affecting the offset shape in a large number of cases involving combinations of two or three of the simple perturbations (Fig. 2B). Shape of the trait in the ancestor and descendant is the same but the descendant arrived at the same shape via a different ontogenetic trajectory. Because there is no truncation or extension of shape in the descendant, this is not paedomorphosis or peramorphosis. We propose the term isomorphosis for cases in which heterochrony does not affect the offset shape. As noted above, we have modified the Alberch et al. (1979) terminology by using deceleration to describe the case of a shift to a slower rate (replacing their 'neoteny'), and hypomorphosis to describe the case of an early offset (replacing their 'progenesis'). For reasons discussed below, we prefer to retain

### Figure 1

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<tr>
<th>Simple Heterochronic Processes</th>
<th>Description</th>
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<tr>
<td><strong>Development is truncated</strong></td>
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<tr>
<td><strong>DECELERATION</strong> (-k)</td>
<td>(negative offset)</td>
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<td><strong>HYPOMORPHOSIS</strong></td>
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<td><strong>Development is extended</strong></td>
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<td><strong>ACCELERATION</strong> (+k)</td>
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<td><strong>HYPERMORPHOSIS</strong></td>
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<td><strong>PRE-DISPLACEMENT</strong></td>
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Figure 1. Six simple heterochronic processes identified by comparing ontogenetic trajectories of ancestral (a) versus descendant (d) ontogenies. Ontogenetic trajectories are defined by rate of shape development (k) from age of onset of growth (α) to the age when the offset shape is attained (β). Arrows on the shape axis indicate patterns of truncated (top) or extended (bottom) development. The terms deceleration and hypomorphosis are formally proposed to replace the inappropriate terms neoteny and progenesis, respectively, used by Alberch et al. (1979). Although originally defined for comparing species (Alberch et al., 1979) this scheme can be used to categorize both inter- and intraspecific heterochronic phenomena.
neoteny and progenesis in their more traditional meanings and thus deceleration and hypomorphosis, respectively, are not synonyms for these terms but new terms to supersede them.

Figure 2. Complex patterns of heterochrony. (A) Paedomorphosis and peramorphosis can result from multiple perturbations of the three developmental parameters, rate, onset and offset. Each of the simple perturbation trajectories (shaded boxes) can be shifted by one, the other, or both of the other two parameters (circles and rectangles). (B) Heterochrony can also occur without affecting the offset shape, which we term isomorphosis for interspecific comparisons. This occurs in a large number of cases (open boxes and light trajectory lines) involving combinations of two or more simple perturbations from the ancestral ontogeny (centre box and heavy trajectory). Shape of the ancestor and descendant is the same but the descendant arrived at the same shape via heterochronically different trajectory. Because there is no truncation or extension of shape in the descendant this cannot be termed paedomorphosis or peramorphosis.
Rejection of neoteny as a term for describing a shift to a lower rate of development

We have two reasons for rejecting the term neoteny as defined by Alberch et al. (1979). First, the original meaning of neoteny was much more general. Over the years the term has been given a series of more restrictive definitions that have led to considerable confusion in the literature. Kollmann (1885) coined the term neoteny to describe the retention of larval features in *Ambystoma mexicanum* and other perennibranch species of salamanders. According to this first definition, neoteny describes species patterns that involve a truncation of development, and thus, is essentially a synonym for paedomorphosis (Gould, 1977). De Beer (1930) used neoteny to describe the acceleration of gonadal development (progenesis of Gould) and (combined with) the retardation of somatic development. Gould (1977: 483) restricted the use of neoteny to “paedomorphosis produced by the retardation of somatic development,” and he did not distinguish whether a shift in rate, onset or offset was involved. Alberch et al. (1979: 304–305) further restricted the definition of neoteny to the specific case of paedomorphosis produced by a decrease in developmental rate (-k) in the ontogeny of the descendant species. In addition, neoteny has often been used to describe variability in the timing of somatic development among individuals within species (e.g. Glass, 1951; Healy, 1970; Eagleson, 1977; Norris et al., 1977). Pierce & Smith (1979) reviewed the use of neoteny and added to the confusion by describing: neoteny (sensu lato) as paedomorphosis and neoteny (sensu stricto) as “larval reproduction via deleted somatic development”, which is yet another definition for neoteny. These various definitions of neoteny, and the major conceptual differences between them, has lead to considerable confusion in the literature making it virtually impossible to use the term unambiguously.

Second, deceleration (Reilly, 1994) is the logical and unambiguous descriptive term for the opposite of acceleration. Deceleration clearly describes the restricted case of a heterochronic shift to a lower rate of development.

Rejection of progenesis as a term for describing a shift to an earlier offset

We have three reasons for rejecting the term progenesis of Alberch et al. (1979). First, the term progenesis has been defined in a variety of inconsistent ways. Giard (1887: 23; cited in Gould, 1977) first used the term for accelerated maturation stating: “We say that an animal exhibits progenesis when sexual reproduction occurs in a more or less precocious fashion, that is to say when the sexual products (eggs or spermatogenesis) form and mature before the animal has attained its complete development.” Giard & Bonnier (1887: 195; cited in Gould, 1977) stated that “we have progenesis when, in normal development with normal growth, the genital organs develop prematurely and allow the animal to reproduce before it has assumed the adult characters.” Both definitions assume that the normal terminal shape of somatic traits will be attained in the normal amount of time and that accelerated development is limited to reproductive traits. As such, progenesis originally had a very clear meaning involving precocious sexual maturation with no necessary changes in somatic development. Thus, Giard’s progenesis was essentially a special case of heterochrony involving accelerated development of reproductive traits to their normal terminal shape in a shorter time. In terms of our model this could be
described as a case of reproductive isomorphosis (by acceleration and hypomorphosis) that results in an earlier offset of sexual maturation in an otherwise ancestrally shaped reproductive system (see Fig. 3D, below).

Gould (1977) presented three definitions of progenesis: (1) “We now designate ... as progenesis those cases of paedomorphosis produced by accelerated maturation and the precocious truncation of ontogeny,” (p. 179); (2) “for accelerated maturation I shall use Giard’s term progenesis,” (p. 226); and (3) “Paedomorphosis produced by precocious sexual maturation of an organism still in a morphological juvenile stage,” (glossary, p. 485). In Gould’s Definitions 2 and 3 the normal timing of somatic development appears to be unaffected by heterochrony and thus, they are similar to the special case of reproductive heterochrony originally defined as progenesis by Giard. Gould’s first definition, however, requires heterochrony in reproductive traits and somatic traits. This definition is not consistent with Giard’s.

Two years later Alberch et al. (1979: 305) restricted progenesis to paedomorphosis produced by an earlier offset time (–β): “A paedomorphic descendant can also be produced by a mutation which decreases the growth period (or limiting signal), ..., a process known as progenesis.” McNamara (1986: 8) explicitly couples progenesis (sensu Alberch et al., 1979) with sexual maturity stating in his definition of progenesis, “If onset of maturity occurs at an earlier stage of development in the descendant, morphological and size changes will be stopped or severely retarded precociously.” Later, he explicitly states, “Progenesis is global, affecting the whole organism” (loc. cit.: 1986: 8). Thus, there is no provision in McNamara’s progenesis for a case where a somatic trait is simply truncated by an earlier offset time.

These various and inconsistent definitions, coupled with the conceptual ambiguity of whether progenesis refers to just reproductive heterochrony, reproductive and somatic heterochrony, or any type of heterochrony involving an earlier offset time, makes use of the term progenesis problematic.

We suggest that much of the confusion regarding progenesis stems from the concept of “terminal shape” and its relationship to somatic and reproductive ontogeny. For example, Alberch et al. (1979) appear to limit progenesis to a negative perturbation of offset time for a given trait (–β), and it is impossible to ascertain whether they clearly separated reproductive from somatic heterochrony in their model because of their ambiguous descriptions of ‘terminal shape’. Whether they meant to or not, Alberch et al. (1979) associate the terminal developmental stages of somatic ontogenetic trajectories (the offset shape) with the presence of sexual maturity, as did De Beer (1930) in his definition of neoteny and as did Gould (1977) in one of his definitions of progenesis (definition 1 discussed above). In describing an ontogenetic trajectory, Alberch et al. (1979: 299) state, “we can follow the growth of a system from its inception to its mature form.” They refer to terminal shapes in somatic traits as “a final, or adult, size” (loc. cit.: 300), “the adult shape” (loc. cit.: figure 10 caption), and “the adult configuration” (loc. cit.: 304). One can only conclude that they meant the terminal shape to be the shape at sexual maturity. There is no requirement for using the shape of a somatic trait at sexual maturity as the offset point for the development of that trait when, in fact, heterochronies of most somatic traits are uncorrelated with maturation of the gonads (Fink, 1982). Herein lies a major point of confusion with both the Alberch et al. (1979) notion of terminal shape and their use of progenesis to describe the simple case of an earlier offset in any trait: by their definition of terminal shape, ‘progenesis’ must involve both an early offset in the somatic trait and the acceleration of gonadal development to match that
offset time. They are describing two distinct, simple heterochronies with the same term (c.f. Fig. 3 overleaf).

Finally, hypomorphosis is the logical and unambiguous descriptive term for the opposite of hypermorphosis. It clearly describes the restricted case of a heterochronic shift involving an earlier offset of development in a particular trait and has no other meanings that could cause confusion. Several workers have already abandoned progenesis sensu Alberch et al., (1979) in favor of the term hypomorphosis (Shea, 1983, 1988; McKinney & McNamara, 1991; Reilly, 1994).

Examples of why the Alberch et al. (1979) ‘terminal shape’ doesn’t work

The first example is taken directly from the Alberch et al. (1979) Model for hypomorphosis (Fig. 3A; their progenesis). The heterochronic change is mapped as the truncation of development of the somatic trait in the descendant (d) by a shift to an earlier offset time (–β̂) along the same ontogenetic trajectory as the ancestor (a). If the terminal shape is ‘the adult shape’ or ‘adult configuration’ as defined by Alberch et al. (1979), then by definition the timing of sexual maturity has to occur at the descendant’s offset time as well (Fig. 3B). Therefore, the truncation of the development of the somatic trait must concurrently involve an acceleration of development of the reproductive system. These confounded heterochronies can be mapped separately as distinctly altered ontogenetic trajectories for the somatic and reproductive traits. The somatic trait remains a case of paedomorphosis by hypomorphosis (Fig. 3C). However, when the heterochrony involving the reproductive system is mapped, a different process is obvious (Fig. 3D). The descendant reproductive system attains maturity (its terminal shape) at an earlier time relative to that of the ancestor, thus, its development has been accelerated. But, because both the ancestral and descendant reproductive systems presumably reach the same terminal shape (i.e. sexual maturity), they are isomorphic in the descendant (Fig. 3D). Furthermore, if the reproductive system is isomorphic, an earlier offset time is required in the descendant as well. Therefore the reproductive system of the descendant exhibits isomorphosis by acceleration and hypomorphosis. Although there may be cases where both somatic and reproductive heterochronies have occurred simultaneously, mapping them separately imparts more information and does not require that one assume the somatic trait of interest is linked to sexual maturity.

The second example involves a familiar model for heterochrony, the Mexican axolotl, Ambystoma mexicanum (Fig. 4). The axolotl holds “the exemplar’s role” (Gould, 1977: 177) as the model for neoteny (sensu Kollman, 1885 = paedomorphosis). It is known for its permanent retention of premetamorphic morphology relative to its sister taxon, Ambystoma tigrinum, and other outgroup taxa from the genus Ambystoma (which undergo complete metamorphosis, Fig. 4A). The complete retention of premetamorphic morphology is evident in most aspects of the head and external anatomy (Reilly, 1994).

The ancestral ontogenetic trajectory of Ambystoma tigrinum, based on head shape change over time, is a curve punctuated into embryonic (E), larval (L), metamorphic (grey boxes) and transformed (T) periods (Fig. 4B and C: solid lines). The ontogeny of Ambystoma mexicanum (dashed lines) follows the ancestral embryonic and larval trajectories to a point in time, after which head shape develops no further. Sexual
maturity occurs at the same age as in the ancestral ontogeny. Thus, *A. mexicanum* permanently retains the premetamorphic somatic form.

Using the shapes at sexual maturity as the offset shapes and connecting these shapes to the origin (following the Alberch et al. Model, Fig. 4B: dotted lines), the somatic morphology of *Ambystoma mexicanum* is categorized as having a decreased rate (-k) relative to the ancestral ontogeny. Therefore, *A. mexicanum* is paedomorphic by deceleration (their neoteny), according to the Alberch et al. Model. However, if one uses the actual times when the terminal somatic shapes occur (when the trajectories asymptote) as the end points of the ontogenetic trajectories (sensu Fink, 1982), a

![Diagram](image-url)

Figure 3. Why the Alberch et al. (1979) 'terminal shape' does not work. (A) Process of hypomorphosis (progenesis of Alberch et al. (1979)) as presented in the Alberch et al. model in which the descendant's shape (d) is truncated relative to the ancestral shape (a). (B) Because the Alberch et al. (1979) definition of 'terminal shape' is shape at sexual maturity, any somatic hypomorphosis of the descendant (d) must be coupled with an acceleration of reproductive development such that the descendant reaches the normal reproductive state at the time of its earlier somatic offset. Reproductive and somatic heterochronies are not necessarily coupled and the resultant somatic hypomorphosis (C) and reproductive isomorphosis (D) should be mapped and considered separately. Note that using terminal shape at sexual maturity as the offset point requires the reproductive system to both develop faster (acceleration) and stop developing sooner (hypomorphosis) on the way to its ancestral shape.
different heterochronic process is revealed (Fig. 4C). The ontogeny of somatic characters of Ambystoma mexicanum exhibits an earlier offset time relative to the ancestral ontogeny (as seen in A. tigrinum). Because there is a negative perturbation of the shape and time offsets, the heterochronic process that results in the premetamorphic (i.e. paedomorphic) morphology of the axolotl head is hypomorphosis.

Figure 4. Cranial paedomorphosis in the axolotl, Ambystoma mexicanum. The axolotl is known for its permanent complete retention of larval head morphology relative to the primitive condition exemplified by its metamorphosing sister taxon Ambystoma tigrinum and outgroups A. Heterochrony in the axolotl is categorized using (B) the shape at sexual maturity (Alberch et al., 1979) and (C) the asymptote of shape development as offsets. The ontogenetic trajectory of the axolotl (dotted line) asymptotes at the larval somatic morphology (L) compared to the ancestral ontogeny (based on Ambystoma tigrinum (solid lines)) which continues through metamorphosis (grey boxes) to the transformed head shape (T). The head shape axis used to quantify ontogenetic trajectories in these species is based on numerous changes in the cranium, hyobranchial apparatus and external morphology (reviewed in Reilly, 1994). Choice of offset shape results in paedomorphosis in the axolotl (indicated by the shape truncation on the Y-axis (arrow)) being categorized as deceleration (B) or hypomorphosis (C). $P_D =$ offset of descendent; $P_A =$ offset of ancestor; Sex. mat. = onset of sexual maturity.
The axolotl is cited widely as the classic example of “neoteny” (Gould, 1977; Raff & Wray, 1989). Obviously, the head of A. mexicanum exhibits an example of neoteny (= paedomorphosis) sensu Kollmann (1885) and Gould (1977), but it does not exhibit an example of neoteny (= deceleration) sensu Alberch et al. (1979).

Fink (1982) and Raff & Wray (1989) also noted the confusion regarding the terminal shape of Alberch et al. (1979) and their usage of neoteny and progenesis. Fink (1982: 257) states, “There is a potential for confusion, however, since the authors use traditional definitions of heterochrony — definitions that employ developmental stages present in adults as reference points”. He also points out that most somatic heterochronies are altered in a manner not correlated with maturation of the gonads and states that it may eventually be desirable to coin new terms to differentiate between the traditional usages (of neoteny and progenesis) and the ones accepted in the Alberch et al. Model. Raff & Wray (1989: 429) point out that “By avoiding explicit comparisons of timing changes during development to gonadal maturation, it is possible for studies of heterochrony to transcend the realm of global morphological events occurring late in development.”

Obviously much of this confusion stems from the imprecise use of words such as ‘juvenile’ and ‘larval’ vs. ‘mature’ and ‘adult’ when referring to earlier, later, or terminal somatic stages. In general, the terms juvenile and larval refer to body forms or somatic stages of development associated with ontogenetic stages before sexual maturity or procreation occurs. Conversely, ‘adult’ and ‘mature’, connote the possession of sexual maturity, and thus, refer to reproductive (and usually terminal) somatic stages. Because the absence of sexual maturity is inherent in both ‘larval’ and ‘juvenile’ these terms should not be used to describe sexually mature (= adult) forms of descendants that retain the earlier ontogenetic somatic morphology of the ancestor. Instead a simple and clear definition of the offset shape of the trait under study should be used. The loose use of these terms is common in biology and they should be avoided when discussing heterochrony. For the remainder of the paper we will follow our definitions of deceleration and hypomorphosis. The terminal shape is simply the offset shape defined by an asymptote in the ontogenetic trajectory of the trait under investigation, not necessarily the shape at sexual maturity.

INTER- VS. INTRASPECIFIC VARIATION IN ONTOGENETIC TIMING

In general, evolution is studied at two levels. On a phylogenetic (interspecific) level, variation among species is used to infer evolutionary relationships, as well as to study the effects that history, the environment, developmental constraints, and other factors have had on the evolution of interspecific variation. On a tokogenetic (intraspecific) level, variation is studied in an attempt to reveal the mechanisms by which intraspecific variation arises, as well as how such variation is influenced by various population-level phenomena. At the phylogenetic level, the focus is on differences between species. At the tokogenetic level, the focus is on differences among individuals within species. For reasons outlined below, it is important that the distinction between these two levels of analysis be maintained, especially in the context of heterochrony.

As used today, heterochrony almost universally refers to phylogenetic differences in the timing of development (Gould, 1977, 1992; Hall, 1984; Wake & Roth, 1989; McNamara, 1986). The explicit phylogenetic nature of ‘heterochrony’ is clearly
stated in the Alberch et al., (1979) Model (Introduction, line 14), and has frequently been emphasized (Fink 1982, 1988, Wake & Roth, 1989; Gould, 1977, 1992; Hall, 1984). Thus, heterochronic analyses are generally used to understand how past phenomena have produced the ontogenetic differences observed among species. However, heterochrony also occurs at the intraspecific level. For example, it is well known that phenotypic variation in the timing of metamorphosis in salamanders is an important adaptive response to environmental perturbations (Istock 1967; Wilbur, 1980). Heterochrony plays an important, if not, central role in producing the morphological plasticity and variation observed among individuals within populations (Hall, 1992; Reilly, 1994). Thus, heterochrony can be thought of in terms of differences among species, or differences among individuals within species (whether ecophenotypic or heritable). A major goal of this paper is to illustrate the critical importance of maintaining the conceptual distinction between inter- and intraspecific patterns and processes of heterochrony. We will do this by (1) illustrating the concept of intraspecific heterochrony with an example of this phenomenon, (2) discussing some of the problems with using the Alberch et al. Model and associated terminology to describe intraspecific heterochrony, and (3) proposing a revised, more precise model with associated terminology for describing intraspecific heterochrony.

An example of intraspecific heterochrony in the salamander Ambystoma talpoideum

The mole salamander, Ambystoma talpoideum, exhibits intraspecific variation in the timing of cranial metamorphosis (Reilly, 1987). The normal species trajectory for head shape in A. talpoideum (Fig. 5; solid line) involves metamorphosis in the first year (Reilly 1987, 1994) similar to the ancestral trajectory observed in sister taxa and outgroups. Thus, we have an hypothesis of the ancestral ontogeny to polarize

![Figure 5. Intraspecific heterochrony in the Mole Salamander. Some individuals of Ambystoma talpoideum (dashed line) exhibit temporal plasticity (delay) in the onset of metamorphosis (large arrow) relative to the normal species trajectory of metamorphosis in the first year of life (solid line). Metamorphosis is delayed for one or more years but virtually all individuals eventually proceed through normal transformation to the terminal shape for this species (T on y-axis). Note that because there is no phyletic shape change the variant individuals cannot be termed paedomorphs. Symbols and axes as in Figure 4. See text for discussion.](image)
heterochronic shifts in variant individuals. Normally, metamorphosing individuals (Fig. 5: solid line) undergo embryogenesis, develop the larval head morphology, maintain this shape while growing for a few months, and then metamorphose into the terrestrial form. Maturity is attained by the end of the first year of life. However, within a few populations of *A. talpoideum*, some individuals exhibit an alternate developmental pathway through metamorphosis (Fig. 5: dashed line). These individuals have the same embryonic and larval trajectories as their metamorphosing cohorts, but delay the onset of metamorphosis for one or more years, with no change in the timing of sexual maturity (Semlitsch, 1985; Reilly, 1987). All individuals eventually do (or can) metamorphose, and thus, all attain the species terminal metamorphosed shape. Comparison of the two ontogenetic trajectories reveal that the developmental mechanism operating here is the temporary delay of the onset of metamorphosis in variant individuals.

Problems with applying the Alberch et al. Model to intraspecific heterochrony

Applying the Alberch et al. (1979) Model to variant individuals within populations poses several difficulties that we will discuss using the example of intraspecific heterochrony in *Ambystoma talpoideum*. First, given the explicit statements that the Alberch et al. Model is designed for interspecific comparisons it would appear to be inappropriate from the start: how do we categorize a pattern where there is no phylogenetic shift in terminal shape (Fig. 5)?

Second, given that we are going to try to use the interspecific model to categorize intraspecific variation can we apply processes explicitly used to describe phyletic transitions in development (the six pure perturbations) to describe ontogenetic differences among individuals? The answer is yes, if we have an hypothesis of the ancestral ontogeny, but the perturbations are only temporary if the individuals eventually continue development and reach the species terminal shape.

Third, what offset shape do you use in intraspecific comparisons? How do we compare the ancestral ‘terminal’ shape to the ‘transient’ and ‘terminal’ shapes of the variant individuals so that the perturbational processes can be determined? These difficulties are illustrated in Figure 6 for the example of delayed metamorphosis in variant individuals of *Ambystoma talpoideum*.

A comparison of the terminal shapes of the ancestral condition (metamorphosis in the first year) to the final (‘terminal’) shapes of the variant individuals (metamorphosis after one or more years) is illustrated in Figure 6A. We observe that the ‘terminal shapes’ are the same in individuals exhibiting the ancestral and variant trajectories but the variants arrive at this shape at an older age. Therefore, the variant individuals have a positive shift in offset time or hypermorphosis. No matter how many years metamorphosis was delayed it would be categorized as hypermorphosis. Because the shift does not result in either a truncated or extended shape it is not similar to the interspecific process of paedomorphosis or peramorphosis, but is similar to isomorphosis.

If the ‘transient shape’ of the variant individuals is compared to the ‘terminal’ shape of the individuals exhibiting the ancestral ontogeny there are three possible interpretations (Fig. 6B,C,D). However, the truncated shape of the variant individuals is only temporary and thus, the processes indicated are transient. Therefore, the variant individuals exhibit a pattern that is temporarily similar to the
Figure 6. Offset shape and problems with categorizing intraspecific heterochrony with the Alberch et al. Model. Using the example of *Ambystoma talpoideum* variant individuals can be categorized as (A) hypermorphic when the final shapes are used, (B) decelerated when the shape at sexual maturity is used (Alberch et al., 1979), (C) hypomorphic when the temporary asymptote is used, and (D) post-displaced and hypermorphic when delayed metamorphosis is used. Symbols and axes as in Figure 4. See text for discussion.
pattern of paedomorphosis observed when comparing two species (Fig. 4C). In the first interpretation, we use the ‘terminal’ shape and linear trajectories of Alberch et al. (1979) to compare the shapes at the onset of sexual maturity (Fig. 6B). In this case the process would be characterized as deceleration (–k). In the second interpretation, we compare the individuals exhibiting the ancestral terminal shape with the transient shape of the variant individuals mapped at the time the variant shape begins (Fig. 6C). In this case the transient offset occurs (at the asymptote) when the larval shape is first attained. Comparing the terminal and transient shapes the process is now categorized as hypomorphosis. In the third interpretation we incorporate knowledge of the developmental mechanism producing the variant trajectories and map only those parts of the trajectories that differ (Fig. 6D). We know that the variant individuals simply delay metamorphosis for one or more years. If we compare the onset (α) and offset (β) of metamorphosis in the individuals exhibiting the ancestral ontogeny to the variants that delay metamorphosis we get yet another interpretation of the heterochronic processes involved. In this case, both the onset and offset of metamorphosis are shifted to the right (with no change in the shape of the trajectory during metamorphosis) and the terminal shape is attained at an older age in the variant individuals. Therefore, two processes produce the temporarily truncated shape in the variants. The onset of metamorphosis is post-displaced and the offset of metamorphosis is hypermorphic, resulting in a delay in the arrival at the species terminal shape. Given these four examples (Fig. 6) then which terminal shapes do we use to identify the process? Obviously, the portion of ontogeny under study and the temporal nature of variant patterns must be explicitly discussed before processes producing intraspecific patterns of heterochrony can be convincingly identified.

A new terminology for intraspecific heterochrony

We propose to expand the Alberch et al. (1979) Model for use on intraspecific heterochrony by presenting a new set of terms to describe developmental patterns and processes observed among individuals within species (Fig. 7). Although the Alberch et al. (1979) framework made no provision for categorizing temporary intraspecific patterns of heterochrony that do not affect offset shape, we see no problems with using the six simple perturbations model to explain intraspecific patterns of heterochronic development if the offset shape is clearly defined (but one has to remember that individual variants may or may not eventually reach the ancestral terminal shape).

Paedotypy, peratypy and isotypy

We propose that variant individuals within species that exhibit truncated development relative to the ancestral ontogeny be termed paedotypic and that individuals with extended development be termed peratypic. Those individuals that eventually reach the ancestral offset shape via a different trajectory are termed isotypic. These terms describe heterochronic patterns observed among individuals within species. The prefixes were chosen to reflect truncated, similar, and extended shapes of variant individuals and they parallel prefixes of terms describing interspecific patterns (paedomorphic, isomorphic and peramorphic). The root ‘typic’
was chosen because it is used in a variety of circumstances to refer to variation in the characteristics of individuals or groups of individuals within species (for example, phenotypic, genotypic, and ecotypic intraspecific variation or holotypes, paratypes, syntypes in taxonomy). The root also makes no necessary allusions to heritable versus nonheritable traits (genotypic versus ecophenotypic variation). Thus, the term paedotypic can refer both to heritable variants (atavisms or neomorphic traits) as well as ecophenotypic departures from the normal (ancestral) ontogeny. For the general terms for processes producing intraspecific heterochrony (to parallel the general processes of paedomorphosis, isomorphosis, and peramorphosis) we propose the terms paedogenesis, peragenesis and isogenesis, respectively (Fig. 7).

Paedogenesis

We use the term paedogenesis for the general process that produces intraspecifically truncated patterns for two reasons. First, the etymology of the word paedogenic describes “truncated patterns that have been generated in individual ontogenies” (Brown, 1956), in the same way that other terms describe processes where environmentally induced phenotypic differences are produced in individuals (e.g. teratogenic, mutagenic, carcinogenic).

Second, the term consistently has been used to describe intraspecific patterns of
truncated development. Von Baer (1866) described the term to describe accelerated maturity in the remarkable parthenogenetic portion of the life cycle of gall midges. These dipterans can reproduce by normal sexual reproduction with a series of larval and pupal molts producing a winged reproductive imago (the ancestral ontogeny), or they can mature and reproduce after the first molt to produce many more offspring in less time. Which reproductive cycle is used is influenced by ecological conditions. Similar ecophenotypic patterns are observed in other insects as well (Scott, 1938; Wyatt, 1967; Rack, 1972; Mitter, 1973) and 'paedogenic' is universally used to describe them. Hamann (1891: cited in Gould, 1977) originally expanded paedogenic to include all intraspecific patterns of precocious maturation in insects and then suggested the possibility that reproduction in the larval state could become phylogenetically fixed in some species (*"phylo-pædogenie" = paedomorphosis), thus recognizing the distinction between intra- and interspecific heterochrony. De Beer (1958) limited the definition of paedogenic to individuals with accelerated maturation with constant somatic development (because he uses paedomorphic to describe interspecific patterns we assume he has used paedogenesis for intraspecific patterns). Thus, the term is used to describe intraspecific patterns of accelerated maturation in parthenogenetic insects that in our terminology are reproductive paedotypes relative to the ontogeny of the sexual portion of the life cycle (and the primitive condition).

Paedogenic has also been used to describe variant individual amphibians that delay metamorphosis (Kollmann, 1885: "giant larvae"; Salthe & Mecham, 1964: "facultative metamorphosis"; Nussbaum, 1976: "non-metamorphic Dicamptodon ensatus"). In this case however, reproductive maturation is normal and somatic development is delayed so the individuals are somatic paedotypes in our terminology. Although paedogenic is used occasionally in the literature to describe interspecific patterns (as a synonym of paedomorphosis), it appears that the term has been regarded almost universally as a descriptor of interspecific patterns of truncated development. We have simply expanded the meaning of paedogenesis to describe any pattern (reproductive or somatic) of truncated development among individuals within species (paedogenic) and the general process that produces such truncated patterns (paedogenesis) whether by deceleration, hypomorphosis or post-displacement.

An example of paedogenesis is illustrated by the intraspecific heterochrony exhibited by *Ambystoma talpoideum* (Fig. 5) discussed above. Individuals that temporarily delay metamorphosis have temporarily truncated somatic development relative to the ancestral condition. These individuals are paedotypic (until they metamorphose and then they are isotypic). Note the distinction: an individual may be paedotypic at time T but not at time T + 1. Species with paedomorphic traits have no such flexibility. Identification of the exact perturbational process that produces paedogenesis in variant individuals depends on the offset shape and portion of the ontogeny used (Fig. 6).

The use of the terms paedotypic/ paedogenesis to describe intraspecific phenomena allows workers to avoid using the interspecific terms paedomorphic/ paedomorphosis. For example many ecologists (e.g. Semlitsch & Wilbur, 1989; Harris et al. 1990; Semlitsch, Harris & Wilbur, 1990; Whiteman, 1994) characterize the pattern of temporarily delayed metamorphosis exhibited by *A. talpoideum* (Fig. 5) as paedomorphosis and the individual variants as paedomorphs and this creates serious semantic confusion. This misuse of the Alberch et al. Model is widely employed to support the interpretation that has become dogma among ecologists (Whiteman,
1994), that individual A. talpoideum have a life history choice between metamorphosis and “paedomorphosis” (Semlitsch & Gibbons, 1985). Only after phylogenesis has occurred can the different heterochronic patterns be considered in phyletic terms such as paedomorphosis.

It is easy to see why the model’s terminology is often misunderstood. Alberch et al. (1979: 306) confuse the issue by using intraspecific developmental patterns of variation as examples for their interspecific heterochronic model! The most blatant example is in their formal definition of post-displacement, where the “creep” fowl genetic abnormality is presented as a “good example” of “paedomorphosis by post-displacement.” This abnormality is an intraspecific genetic defect.

Furthermore, although Gould (pers. comm.) has confirmed that his entire volume (1977) was couched entirely in terms of interspecific heterochrony, he confused the issue by repeatedly mixing intraspecific examples of heterochrony in many of his discussions. For example, in the section discussing “amphibian neoteny” Gould uses “facultative paedomorphosis,” “paedomorphic,” “paedomorphosis by larval reproduction,” “neotenic,” and “paedogenes” to describe intraspecific variation in the timing of metamorphosis in salamanders (pp. 319–321). As we have shown above and has been emphasized elsewhere (Wake & Roth, 1989; Gould, 1977: 181, 1992), paedomorphosis is not appropriate for individuals within species.

This confusion of intra- and interspecific heterochrony has forced workers into adopting such terms as ‘facultative,’ and ‘obligate’ paedomorphosis. Given the Alberch et al. (1979) definition of paedomorphosis, we consider the term ‘obligate paedomorph’ to be a tautology (redundant) and ‘facultative paedomorphosis’ to be an oxymoron.

**Peragenesis**

The term peragenesis is proposed for the general process of extending development among individuals within species. It was chosen to parallel the term peramorphosis. An apparent example of peragenesis can be seen in the heads of male salmon from the genus Oncorhynchus. Males undergo morphological transformation during breeding just prior to death. During this transformation, cranial hypertrophy produces beak-like jaws. Females do not undergo this dramatic transformation. Thus, at this intraspecific level, within this species the males are peratypic relative to females in head shape. Hypermorphosis of the head apparently is induced by an increase in male sex hormones when the individuals return to freshwater to spawn. Because male cranial ontogenetic trajectories are extended beyond the female trajectory, this appears to be a special case of intraspecific heterochrony, sexual heterochrony. This case raises some interesting questions regarding the origin of sexual dimorphism. In many species that exhibit sexual dimorphism the female condition is the ancestral one. For example, females and juveniles of both sexes from members of the Fundulus notti group of North American topminnows (Cyprinodontidae) have similar color patterns, while adult males differ (Wiley, 1977). It may be that most sexual dimorphism is the result of peragenesis in the males (but see Bjorklund (1991) for an example of female paedogenesis). When we consider interspecific variation among salmonid species, male snout hypertrophy is derived among the salmonids (absent among outgroups). Therefore, hypertrophic males are peratypic relative to conspecific females but peramorphic relative to species with no...
Individuals that attain the species offset shape via a different ontogenetic trajectory are termed isogenic. For example, variant Ambystoma talpoideum are paedogenic until they metamorphose, at which time they are the product of isomorphosis (Fig. 6A).

**LEVELS OF ANALYSIS AND THE LIMITS OF HETEROCHRONIC MODELS**

Heterochrony has been described in terms of 'global' and 'local' levels on both the shape (whole organism shape vs. coupled or single traits) and time (all or part of the ontogeny) axes. Comparative biologists usually study entire ontogenetic trajectories where the onset point is the beginning of ontogeny and the offset point is the final shape that obtains (e.g. see papers in McKinney, 1988). Developmental biologists, on the other hand, generally focus on early segments of ontogeny where heterochrony produces embryological or early ontogenetic differences. On this level, the genetic and mechanistic bases of development are the focus of the analysis (Raff & Wray, 1989) and the early perturbations may or may not affect the subsequent or, final shape of the traits under study. Developmental biologists have argued convincingly that general utility of the heterochrony paradigm depends on extending the conceptual bounds of heterochrony beyond global events (Raff & Wray, 1989). As long as traits are explicitly defined and asymptotes are used to define the onset and offset points, any portion of shape ontogeny can be clearly delineated for study at most levels of analysis. However, at the lowest level of analysing developmental mechanisms, the heterochrony models may break down as discussed below.

To illustrate the influence of level of analysis we examine the well-documented case of direct development in sea urchins of the genus *Heliocidaris* (Williams & Anderson, 1975; Raff, 1987; Raff & Wray, 1989; Wray & Mclay, 1989; Raff, Parks & Wray, 1990). In Figure 8 the phylogenies (A) and ontogenies (B) of two well-studied sister species of sea urchins are compared. One species exhibits the ancestral ontogeny (*Heliocidaris tuberculata*) and the other has early developmental perturbations that result in an accelerated development to the terminal shape (*H. erythrogramma*). *Heliocidaris tuberculata* exhibits the primitive ontogeny for sea urchins (Raff, 1987). The eggs develop into a planktonic feeding pluteus in about 3 weeks. The pluteus larva has a characteristic 'spiked' shape from elaborate internal skeletal elements projecting into arms surrounding the mouth and gut. After several weeks of feeding, the pluteus larva settles and metamorphoses within two days into a juvenile sea urchin. The juvenile sea urchin gradually attains the 'terminal' sea urchin shape in about 20 days (Fig. 8B).

*Heliocidaris erythrogramma* eggs develop into a morphologically different, non-feeding larvae that live for about 2 days before metamorphosing into the typical juvenile sea urchin. Its ontogeny from the onset of metamorphosis to the terminal sea urchin shape is essentially identical to the primitive condition observed in *H. tuberculata* except that it occurs much earlier. Metamorphosis to the juvenile sea urchin occurs in 5 days in *H. erythrogramma* compared to weeks later in *H. tuberculata*. The terminal
shapes of the two species are identical except for differences in the cross-sectional shapes of the urchin's spines (Clark, 1946; Dakin, Bennet & Pope, 1966). Developmental studies (reviewed in Raff, 1987) have shown that the radically different shape and short, non-feeding lifespan of the *H. erythrogramma* larvae is due to the fact that no skeleton or functional gut forms in the developing embryo. Thus, the reduction or elimination of these larval structures is accompanied by an acceleration of processes that give rise to the juvenile sea urchin several weeks earlier than in the ancestral condition.

Several points can be made regarding the occurrence of heterochrony during specific portions of the ontogeny of these sea urchins. First, there are no differences in timing from first cleavage to the beginning of gastrulation, therefore heterochrony is not 'global' on either the shape or time axes. At the whole ontogeny level, the terminal body shape of *H. erythrogramma* is isomorphic because the terminal body shapes of the two species do not differ (Clark, 1946; Dakin et al., 1966), but the ontogenetic trajectories do. Third, after the onset of metamorphosis the ontogenetic trajectories are parallel. Thus, *H. erythrogramma* is isomorphic by pre-displacement and hypomorphosis. If one examines the ontogeny between the beginning of gastrulation and when larval shape change ceases, the larval morphology of *H. erythrogramma* is accelerated and hypomorphic. However, because the larval shape of *H. erythrogramma*

![Figure B. Heterochrony in a direct developing sea urchin. (A) Molecular phylogeny of *Heliocidaris* species and outgroup (Raff et al., 1988). (B) Ontogenetic trajectories for *Heliocidaris* sister species which are essentially identical after metamorphosis begins but shifted in time. See text for discussion.](image-url)
is different than any shape observed in the ancestral ontogeny, the larval shape of *H. erythrogramma* is autapomorphic. Thus, larval shape is not paedomorphic or isomorphic, but is neomorphic. During this part of the ontogeny body shape defies categorization by the Alberch et al. Model because, by definition, truncated descendant offset shapes must pass through earlier ancestral shapes in order to be plotted on the same shape axis.

However, some heterochronic inference may be possible in explaining the loss of portions of development that affect the body shape. Evidence of intraspecific variation in skeletal development in other direct developing sea urchins shows that the larval skeleton is initiated at the normal time, develops to various degrees, but never becomes fully elaborated (variably 'spiked' forms are observed within species); thus skeletal development is variably hypomorphic. This suggests that the development of the skeleton of *H. erythrogramma* may have been 'lost' by collapsing the offset point to the onset point of skeletal formation. Thus, it may be possible to explain the loss of the entire developmental pathway for the skeleton in heterochronic terms as loss by hypomorphosis. If this is true, then the observed heterochronic pattern of predisplacement of the entire post-larval trajectory in *H. erythrogramma* is caused by loss of the skeleton by hypomorphosis. Thus, a negative shift of an offset point (of skeletal development) produces what appears to be a negative shift in an onset point (of metamorphosis) and a neomorphic larva has evolved.

A similar breakdown of the heterochrony model occurs when comparing patterns and developmental processes in salamander metamorphosis. It is likely that a pattern like the temporary delay of the onset of metamorphosis in variant individuals of *Ambystoma talpoideum* could have become permanently delayed in an independent lineage as it apparently did in *A. mexicanum*. Comparisons of the ontogenetic trajectories of *A. mexicanum* and variant individuals of *A. talpoideum* with their ancestral ontogenies reveals that both are described as hypomorphic (Figs 4B and 6C). However, if we consider the developmental mechanism involved, variant individuals of *Ambystoma talpoideum* display postdisplacement of onset of metamorphosis and therefore, delay the offset of metamorphosis (Fig. 6D). Thus, the observed pattern of paedomorphosis by hypomorphosis in *A. mexicanum* may have been caused by the loss of metamorphosis by permanent postdisplacement of the onset of metamorphosis in its ancestral lineage. In this case the intraspecific pattern apparently pre-adapted to become an interspecific pattern involves different parameters (onset vs. offset) and directions of change (temporary postdisplacement vs. hypomorphosis), thus knowing one you cannot simply predict the other. Obviously, detailed developmental data are necessary in order to use heterochronic models to describe the specific developmental bases of changes in ontogeny, especially when it involves losses of developmental pathways.

**The Interface Between Interspecific and Intraspecific Heterochrony**

The paradigm of heterochrony has emerged as a central method to document development as an evolutionary force. Gould (1992) recently reviewed the history of the term heterochrony and described how confusion and misunderstanding have molded its modern meaning. Haeckel coined the term heterochrony in the early days of the 'biogenetic law' to describe exceptions to true recapitulation. The falsification
of the biogenetic law in the late nineteenth century had the effect of transforming Haeckel's heterochrony from confusing exceptions (to recapitulation) to a widespread and fundamental process. In the second transformation De Beer (1930), in an act of "creative confusion" (Gould, 1992), redefined heterochrony to apply to shifts in timing of an organ relative to the same organ in an ancestor. In this radical redefinition, de Beer (1930) made heterochrony a general term for phylogenetic change in developmental timing (Gould, 1992). De Beer's redefinition of heterochrony as an interspecific concept (rather than an intra-individual concept) has prevailed based on the models of heterochrony widely accepted today (Gould, 1977; Alberch et al., 1979; Fink, 1982, Wake & Roth, 1989).

With the recent drive toward integration in evolutionary biology, the interspecific model of heterochrony has been applied (with little success) to intraspecific patterns and processes, as well as to lower levels of analysis. Once again confusion has emerged and forced a redefinition of heterochrony to include intraspecific patterns and processes. The general utility of the heterochrony paradigm in evolutionary biology depends on maintaining the conceptual and terminological distinctions between intra- and interspecific phenomena. From the start Gould (1977) and Alberch et al. (1979) confused the issue by explicitly defining their models as interspecific and then using intraspecific heterochronies as key examples. We propose that the established terms for interspecific patterns and process be maintained (with some exceptions, e.g. neoteny and progenesis) and that the alternatives we present (Fig. 7) be adopted for describing intraspecific heterochronies. We have also expanded the model to include heterochronies that do not change the offset shape.

Our modifications are essential to maintain the distinction between inter- vs. intraspecific heterochronic patterns and processes because they are conceptually different (Hennig, 1966). Within species a variety of heterochronies produce developmental differences among individuals. These differences may or may not be heritable. Heritable heterochronies, like any other heritable character, can interact in tokogenetic, microevolutionary processes (such as selection, drift, etc.), being lost, fixed, or variable, as the case may be. The point is that intraspecific heterochrony is the source of variation that can result in interspecific heterochrony. Thus, it is the interaction of intraspecific heterochrony and phylogenesis that produces the interspecific patterns of heterochrony we observe.

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