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DIFFERENT PATHWAYS IN ARTHROPOD POSTEMBRYONIC DEVELOPMENT

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Abstract.—To investigate the consequences of canalization and plasticity in arthropod developmental pathways, we developed a model that predicts eight possible combinations among three larval developmental parameters. From the descriptions of insect and spider postembryonic development, it is apparent that not all aspects of juvenile development are plastic and that species differ in which traits are plastic. Most strikingly, only four of the possible eight combinations of canalized and plastic parameters have been found in nature. Using this model, we show that the identity of the canalized developmental parameters and the degree of genetic variation in the value at which a given parameter is fixed have important implications for the ecology and evolution of complex life cycles.

Key words.—Arthropods, canalization, constraint, growth, plasticity, postembryonic development.

The age and size at which an individual becomes mature are very important determinants of its fitness, and the ultimate, evolutionary causes of variation in both have long attracted attention (e.g., Stearns 1992 and references therein). Both genetic variation and environmentally induced variation (plasticity) can significantly alter the age and size at which an individual matures, but the ecological and evolutionary consequences of genetic versus plastic causes of variation are very different (Caswell 1983; Via and Lande 1985; Gomulkiewicz and Kirkpatrick 1992). Environmentally induced differences among adults are important measures of plasticity (e.g., Stearns and Koella 1986; Solbreck et al. 1989; Hillesheim and Stearns 1991), but these are emergent properties of the juvenile developmental parameters. The relative importance of genetic variation and plasticity in determining age and size at maturity can be better understood by investigation of juvenile development (Schmalhausen 1949; Reznick 1990; Gomulkiewicz and Kirkpatrick 1992; Bernardo 1993). In complex life cycles, juvenile developmental plasticity may play a vital role in the interaction of the life cycle with temporal and spatial variation in habitat quality. However, not all aspects of development are plastic; some are canalized. Species and populations differ in which traits are plastic, and such differences can significantly affect the ability of the organism to compensate for poor growing conditions. In the model of juvenile development presented herein, we describe different combinations of canalized and plastic developmental parameters found in arthropods, and we discuss the ecological and evolutionary consequences of various patterns of plasticity.

Arthropods are ideal for life-history studies because growth and developmental stage are easily quantified. The juvenile period is broken into discrete stages (instars). In most insects and spiders, growth is determinate, and the molt into the adult stage is the final molt, after which the sclerotized body parts grow no further. Thus, size at maturity is determined by the number of stages and growth in each molt. Likewise, the number and duration of the juvenile stages determine the age at maturity. Therefore, any variation (ge-

netic or plastic) leading to maturity at a different size or age will have definite and measurable fitness consequences. Despite the potential importance of phenotypic plasticity in the ecology and evolution of growth curves (e.g., Wilbur and Collins 1973), most students of insect life cycles have concerned themselves primarily with the role of genetic variation (e.g., Tauber and Tauber 1978; Neumann 1986; Bradshaw 1986; Dingle 1986; Venogradova 1986; Roff 1986). What is ignored by many models of arthropod life cycles is that the presence of developmental plasticity may, on an ecological time scale, affect the ability of a juvenile organism to respond effectively to environmental cues and, on an evolutionary time scale, influence the evolution of responses to seasonality (Schmalhausen 1949, pp. 76–77; Schlichting and Levin 1986; Wise 1987; Gomulkiewicz and Kirkpatrick 1992).

To examine the effects of canalization and plasticity in developmental parameters, we developed a heuristic model of eight possible combinations of juvenile developmental parameters (excluding the more complex cycles of aphids and parasites, and those involving larval diapause). We then undertook a search of the literature of insect and spider postembryonic development and found concrete examples of four of the eight possible combinations of plasticity in developmental pathways. We show that, in seasonal environments requiring escape in time or space (diapause or migration), the ability to achieve the appropriate stage by the end of the season will depend upon which aspects of development are plastic. The identity of the canalized parameters, and the degree of genetic variation in the value at which a given parameter is fixed, have important implications for the evolution of both the growth curves and complex life cycles.

DEFINITIONS

The term "plastic" has evoked much confusion in recent discussions, particularly in the literature on life cycles. In studies of insect life cycles, the concept of "plasticity" is frequently used as a synonym for genetic variation within a population, leading to such confusing terminology as "genetic flexibility" and "genetic versatility" (e.g., Masaki 1978; Dingle 1986; Venogradova 1986). In ecological studies of development, "plastic" means any environmentally in-

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duced change in morphology, commonly measured as a shift in the age or size at maturity (Stearns and Koella 1986; Stearns 1992). Most broadly, the term describes an aspect of the biology of an organism that is conditional on the environment (Schmalhausen 1949, ch. 3C; Bradshaw 1965; Smith-Gill 1983; West-Eberhard 1989). The responses of a plastic character may or may not be, strictly speaking, "adaptations" in that they do not necessarily lead to increases in relative or absolute fitness.

To some degree, "plastic" is best defined in contrast to "canalized," and these conditions are actually end points of a continuum. As presented by Smith-Gill (1983), plasticity can vary in degree from totally responsive to the environment, to bounded by maxima or minima, to expression of switches from one developmental pathway to another. For simplicity, we will restrict our discussion to plasticity and canalizaton in growth and development of an individual and will use the term plasticity to refer to unbounded environmentally induced variation. Thus, the existence of maxima or minima in a character or a switch between developmental pathways are degrees of developmental canalization. The patterns of canalization described in this model may or may not reflect developmental constraints as defined by Maynard-Smith et al. (1985), Levinton (1988), and Hall (1992). Note that the definitions below assume some understanding of the natural environment of the study organism and exclude pathological responses to presumably unusual circumstances such as irradiation.

Plastic.—Varying in response to environmental changes such as reduction or temporary absence of food. Changes that are outside of the normal range of physiological conditions and induce morbidity or mortality are excluded. The range of possible responses is determined genetically and may vary among individuals (Schmalhausen 1949; Schlichting and Levin 1986; Hillesheim and Stearns 1991).

Canalized.—Not varying in an individual in response to environmental changes that are within the normal range of physiological conditions. The less variable the phenotype is, the stronger is the degree of canalization (after Levinton 1988; see also Hall 1992, p. 168). Strongly canalized characters will be invariable despite both environmental and genetic variation (Waddington 1966; Levinton 1988). For our purposes, the value of a canalized parameter, for example, the maximum duration of a larval instar, is assumed to be genetically determined and may be correlated with some other aspect of the individual's biology such as its size or sex. Variation among individuals in the value of a parameter necessarily reflects genetic variation. In some cases, canalization is expressed as a fixed value, such as the number of juvenile molts in many hemiptera. More often in arthropod postembryonic development, the canalization is expressed as a maximum or minimum value. We will refer to parameters expressing this type of canalization as "bounded." Although all parameters of development are biomechanically or physiologically bounded under extreme conditions, the bounds reported here have been observed under normal conditions.

Postembryonic development in arthropods can be characterized by several interdependent parameters. The following terminology will be used throughout this discussion:

Size.—The dimensions of the sclerotized body parts that do not change except during ecdysis (Dyar 1890). Commonly, size is measured as head-capsule width in the larvae of holometabolous insects, and leg-segment or carapace dimensions in juvenile hemimetabolous insects and spiders. "Size" has been used to refer to weight in some studies (e.g., Blakley and Goodner 1978; Nijhout 1981).

Weight.—The mass of the juvenile, changing with feeding or starvation during the intermolt interval. Often, actual mass is used; in some arthropods abdomen length, width, or volume can be substituted. This is because the cuticle of the abdomen is soft, and the abdomen expands to hold growing tissues during intermolt weight gain. Note that, in most juvenile arthropods, the measurement of total body length confounds the parameters of size, as herein defined, and weight.

Number of juvenile instars.—The number of juvenile stages that the organism passes through before either pupating (in holometabolous insects) or molting to sexual maturity (in hemimetabolous insects and spiders).

Intermolt interval.—The length of time from one ecdysis to the next (Scriber and Slansky 1981).

Change in size at ecdysis.—The change in the size of the sclerotized body parts when the juvenile molts to the next instar (Dyar 1890).

Premolt weight.—The weight achieved prior to ecdysis. This parameter is highly correlated with the change in size at ecdysis (Beck 1950; Nijhout 1981; Higgins 1992). If only one of the two parameters is reported, plasticity or canalization in one is assumed to indicate a similar condition in the other. Despite this correlation, these parameters are treated independently because it is possible that an organism might gain weight beyond necessary premolt weight that would be stored rather than expended as increased growth in size at ecdysis.

These parameters are interdependent. Premolt weight and intermolt interval are frequently functions of size, therefore increasing during development. Similarly, the number of juvenile instars may be affected by the change in size at ecdysis: animals that grow less at ecdysis will go through additional stages to reach a given size (Sehnal 1985). These interactions are often mediated by the rate of weight gain. However, the rate of weight gain is not considered to be descriptive of the developmental pathway because it is always plastic and dependent upon diet. The relationship between the rate of weight gain, age at maturity, and size at maturity varies among organisms and is dependent upon the developmental pathway.

Three developmental parameters are primarily responsible for determining age and size at maturity: change in size at ecdysis, intermolt interval, and number of instars. Age at maturity is a function of the number of instars and the intermolt interval; size at maturity is a function of the number of instars and the change in size at ecdysis. Fixing either pair of these three characters is equivalent to fixing either age or

TABLE 1. Eight possible combinations of the juvenile parameters determining age and size at maturation or pupation. Bold letters indicate combinations reported in the literature.

		Change in size at ecdysis			
		Canalized N. juvenile molts		Plastic N. juvenile molts	
		Canalized	Plastic	Canalized	Plastic
Intermolt interval	Canalized	X1	X2	F	**A**
	Plastic	E	C	**B**	**D**

size at maturity. Similarly, bounds on either pair of these three characters sets a maximum or minimum for age or size at maturity.

It is also often the case that special restrictions exist for successful pupation or maturation beyond the last juvenile instar (referred to in the arachnological literature as the penultimate instar, in the entomological literature as the ultimate instar). These are manifested primarily as bounds of minimum size (threshold size or constitutive size; Nijhout 1975; Sehnal 1985) and minimum premolt weight (critical size or critical weight; Nijhout 1975; Sehnal 1985). The minimum premolt weight for pupation or maturation is a function of the size achieved in the last juvenile instar (Nijhout 1975). These constraints may be found even when there are no similar restrictions influencing juvenile molts in the same species.

FOUR POSTEMBRYONIC DEVELOPMENTAL TRAJECTORIES

Among the three juvenile developmental parameters that yield variation in age and size at maturity, number of instars, intermolt interval, and change in size at ecdysis, there are eight possible combinations of canalization and plasticity (Table 1). One of these trajectories is completely plastic (D), three have one parameter that is canalized (A, B, and C), three have two parameters canalized (E, F, and X1), and one represents an entirely canalized trajectory (X2).

There are nearly complete data on postembryonic development for 12 species of insects and spiders (Table 2) and incomplete data for several other species. The postembryonic developmental pathways described for these organisms fall into four of the eight possible trajectories, A, B, C, or D. These are the pathways with one or no canalized parameters, allowing both age and size at maturity to vary in response to environmental conditions. Bounds of maxima or minima are much more common than fixed values, and pathways with such partial canalization still allow some variation in the canalized parameter. Although the literature on insect life cycles is extensive, most studies report data for only one or a few larval growth parameters or they exclude experimental manipulations. Without experimental manipulations, it is impossible to distinguish plasticity from genetic variation.

A. *Canalized Intermolt Interval* (Fig. 1A).—Two lepidoptera, *Manduca sexta* and *Pyrausta nubilalis,* and the dermestid beetle *Trogoderma glabrum* exhibit wide variation in the growth at ecdysis and the number of juvenile molts while the maximum duration of the intermolt interval is canalized (Beck 1971a,b, 1972, 1973; Nijhout 1975; Nijhout and Wil-

TABLE 2. Documented and implied variation in juvenile development under controlled environmental conditions (environmental variables studied are listed as Variable(s)). C, canalized; P, plastic.

	Lepidoptera				Coleoptera	Odonata	Hemiptera		Araneae		
	Manduca sexta[1]	*Galleria mellonella*[2]	*Spodoptera littoralis*[3]	*Pyrausta nubilalis*[4]	*Trogoderma glabrum*[5]	*Enallagma hageni, E. aspersum*[6]	*Rhodnius prolixus*[7]	*Oncopeltus faciatus, O. cingulifer c.*[8]	*Nephila clavipes*[9]	*Lycosa T-insignita*[10]	*Linyphia triangularis*[11]
Variable(s)	Food	Food	Temperature	Food	Food	Photoperiod temperature	Food	Food	Food	Food	Food
N. juvenile molts	P	P	P	P	P	P	C = 5	C = 5	P	P	C = 4
Intermolt interval	C max.*	P	P	(C max.)	(C max.)	P	P	P	P	P	P
Δ size/ecdysis	P	(P)†	(P)	P	P	P	(C min)	P	C	P	P
Premolt weight	P	P	P	(P)	(P)	(P)	C min	C min.	C min.	(P)	P
Syndrome	A	D	D	A	A	D	B-E	B	C	D	B

[1] Nijout and Williams 1974; Nijout 1975; Safranck and Williams 1984.
[2] Allegret 1964.
[3] Bhatt and Bhattacharya 1976.
[4] Beck 1950.
[5] Beck 1971a,b, 1972, 1973.
[6] Igram and Jenner 1976.
[7] Wigglesworth 1934.
[8] Blakley and Goodner 1978; Nijout 1979; Dingle et al. 1980.
[9] Higgins 1992, 1993, 1995.
[10] Miyashita 1968.
[11] Turnbull 1962.

* Bounds: max: maximum is constrained; min: minimum is constrained
† Parenthesis indicate that the condition is implied but not explicitly presented in the data.
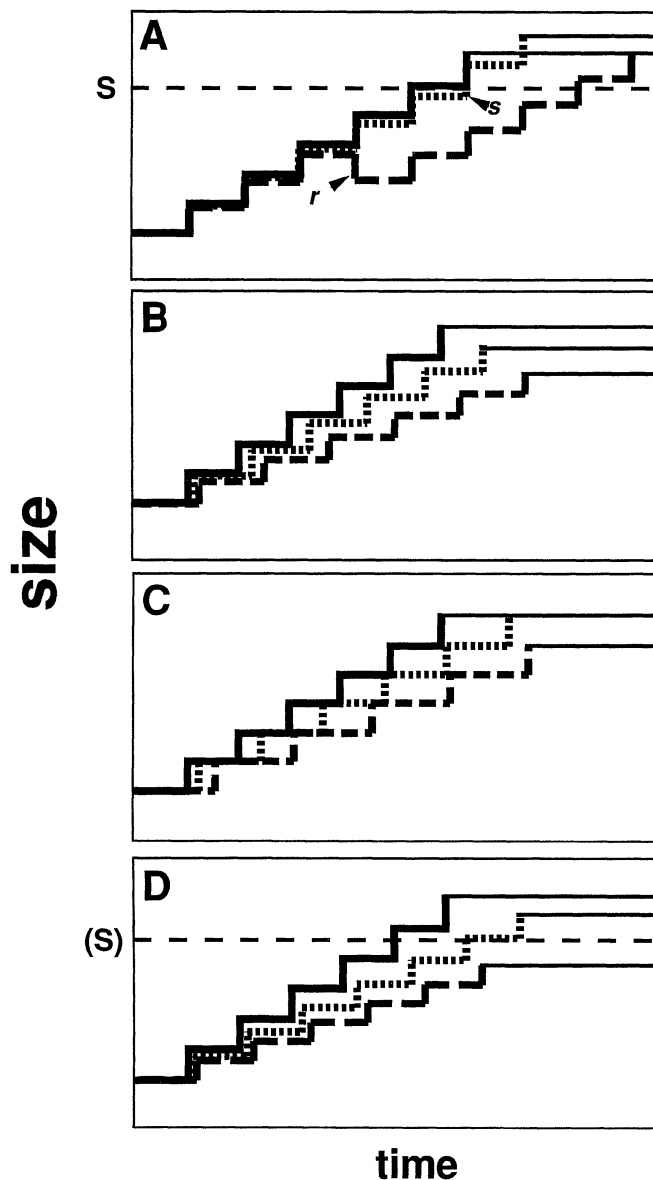
size

time

FIG. 1.   The response to poor conditions will depend upon the type of canalizations present in the system. In each case, the heavy solid line represents the best growing conditions, the heavy dotted line represents intermediate conditions, and the heavy dashed line indicates poor conditions. The thin lines at the end of each pathway indicate the pupal (holometabolous) or mature stage (hemimetabolous). (A) When the intermolt interval and the minimum size for pupation (S) are fixed, the juveniles may undergo supernumerary (s), and retrogressive molts (r). Age at maturity will vary more than size. (B) When the number of molts is fixed, the juveniles will spend longer in each instar, and grow less at each molt. Both age and size at maturity will vary, but the degree of variation in the latter will depend upon constraints in the size for maturation. (C) If the growth per molt is fixed, the intermolt intervals will vary, and the age at maturation will vary more than size. If the number of juvenile molts is variable, then both age and size at maturity will vary. (D) If no developmental parameters are fixed, then both age and size at maturity will vary freely. In some cases, there may be a minimum size for pupation or maturation (S).

liams 1974a,b; Safranek and Williams 1984a,b). Although the data from Beck (1950) are unclear concerning the presence of a maximum intermolt interval in *P. nubilalis,* he reports molts accompanied by zero or negative change in size; such molts strongly imply the presence of maximum intermolt intervals.

In all three species, under high food levels, the larvae gain weight rapidly, molt frequently, and pass through a characteristic, consistent number of instars before pupation. But when food resources are limited, individuals molt after a certain maximum number of days even if no weight gain has occurred. An individual then exhibits a stationary or retrogressive molt to the same or a smaller size.

In this group, extra restrictions were observed for pupation. The larvae must reach a minimum size and minimum weight in order to pupate, and failure to reach this size or failure to achieve the minimum weight during the stage after minimum size was reached resulted in additional "supernumerary" instars. The dermestid beetle requires certain social cues as well as minimum size for pupation (Beck 1971b, 1972). For *P. nubilalis,* the report of supernumerary molts on poor diets indicates the existence of minimum prepupation weight or size (Beck 1950). In all of these species, the ability to undergo supernumerary molts can result in the counterintuitive observation from many studies that larvae reared under poor food conditions or lower temperatures pupate at a greater size than those raised under good conditions (Fig 1A).

B. Canalized Number of Stages (Fig. 1B).—In the milkweed bugs *Oncopeltus fasciatus* and *Oncopeltus cingulifer cingulifer,* the blood-feeding bug *Rhodnius prolixus,* and the spider *Linyphia triangularis,* the number of juvenile instars is fixed whereas the intermolt interval and change in size at ecdysis are plastic, apparently reflecting the rate of weight gain and the premolt weight of each instar (Wigglesworth 1934; Turnbull 1962; Blakley and Goodner 1978; Nijhout 1979). In these organisms, no retrogressive molts have been reported.

The actual classification of *O. fasciatus, O. c. cingulifer,* and *R. prolixus* is ambiguous. The premolt weight is bounded by a minimum (Blakley and Goodner 1978; Nijhout 1979) that apparently reflects requirements of both food volume and nutritional value (Wigglesworth 1934). Variation in growth per ecdysis is generated by variation in weight gain beyond the minimum weight required for molting; for example, the animals can continue eating after achieving the minimum premolt weight. Researchers have reported growth per molt to be plastic in both *Oncopeltus* species (Blakley and Goodner 1978; Nijhout 1979); however, because the change in size at ecdysis depends on the premolt weight, there should be a bound of minimum growth per ecdysis. Wigglesworth does not report measures of growth per ecdysis for *R. prolixus,* but he does mention a "requisite degree of growth" (1934, p. 217), perhaps referring to a lower bound. These hemiptera may represent a fifth, more canalized developmental trajectory (E); the data currently available are inconclusive.

In none of these four organisms is there an indication of additional constraints for molting to maturity. However, the reported sterility of very small individuals of *L. triangularis* (Turnbull 1962) indicates the existence of a minimum size or weight requirement for successful reproduction. Failure to

achieve minimum critical weight for molting to sexual maturity has not been reported to yield supernumerary molts in these organisms, and last-instar juvenile *O. c. cingulifer* on insufficient diets can survive up to four times the normal total developmental time without molting (Blakley and Goodner 1978).

C. Canalized Growth per Ecdysis (Fig. 1C).—In one spider, *Nephila clavipes,* the canalized postembryonic developmental parameters reported are fixed, size-specific change in size at ecdysis and premolt weight (Higgins 1992, 1995). The canalization is expressed more strongly in larger instars than in the first three (Higgins 1993). Rapid weight gain is correlated with short intermolt intervals rather than with increased premolt weight and increased change in size at ecdysis. Slow weight gain is not accompanied by stationary or retrogressive molts but by increased intermolt intervals. The size achieved at sexual maturity is highly variable, reflecting variation in the number of juvenile instars (pers. obs.). Rapidly growing individuals go through more instars and achieve a larger size before maturing. These additional molts are not the same as the supernumerary molts observed in organisms in trajectory A, as they reflect molts beyond a minimum size rather than failure to achieve that minimum. There is no report of a minimum size for molting to sexual maturity, but mature females smaller than the average size of the eighth instar have not been observed (pers. obs.).

D. Fully Plastic (Fig. 1D).—Five species, the moths *Galleria mellonella* and *Spodoptera literalis,* the damselflies *Enallagma hageni* and *Enallagma aspersum,* and the spider *Lycosa T-insignita,* do not exhibit canalization in any of the juvenile developmental parameters (Allegret 1964; Ingram and Jenner 1976; Bhatt and Bhattacharya 1976; Miyashita 1968). Variation in growth per ecdysis and number of molts have been documented, and retrogressive molts have not been observed, which implies that there is no maximum intermolt interval. However, juvenile damselflies held under "winter" conditions can undergo stationary molts (Ingram and Jenner 1976), indicating that there may be special developmental adjustments to overwintering. The other organisms in this group were not subjected to similar experimental conditions.

Data concerning requirements for maturation and reproduction are not available for most of these species. Larvae of *G. mellonella* sometimes undergo supernumerary molts, implying a minimum size and weight for molting to the pupal stage (Allegret 1964). The intermittent expression of this restriction may indicate that there is genetic variation or uncontrolled environmental influences in its expression. Although not termed supermumary molts, additional instars in juvenile *L. T-insignita* are associated with low feeding levels and small size and may also represent failure to achieve a necessary minimum size for maturation (Miyashita 1968). Allegret (1964) reports sterility in very small *G. mellonella* reaching maturity, so ability to pupate or mature at a small size does not necessarily result in reproductive success.

Patterns of canalization in postembryonic developmental pathways described for several other organisms allow them to be fit into one of these four trajectories, despite incomplete data sets. Some studies are observational, and these classifications must be confirmed by laboratory experiments to determine that there is indeed no plasticity in a given de-

velopmental parameter. Most data sets lack information concerning the change in size at ecdysis, preventing distinction between trajectories B and E or between C and D.

A large variety of hemipterans and spiders have fixed number of instars, fitting either trajectory B or E. The hemipteran *Podisus maculiventris* is reported to always have five juvenile instars and a variable intermolt interval dependent upon diet (Mukerji and LeRoux 1969). Five juvenile instars are also found in the milkweed bug *Lygaeus kalmii* (Hunt and Shappirio 1973), in several other species of *Oncopeltus* (Dingle et al. 1980), and perhaps in nearly all hemiptera (H. Brailovsky, pers. comm. 1993). Circumstantial evidence from various species of passalid beetles (M. L. Castillo, pers. comm. 1993) and from spiders in diverse families (Seligy 1971; Toft 1976, 1983; Miyashita 1988) indicates that this developmental trajectory is common.

There are fewer concrete examples of trajectory C, probably reflecting the lack of data concerning growth per ecdysis. Two other spiders, *Nephila maculata* and *Argiope appensa* appear to fit trajectory C, having canalized change in size at ecdysis, variable number of juvenile instars and variable intermolt duration (pers. obs.). The thomisid spider *Thomisus onustus* has diet-dependent variation in the number of instars and intermolt duration but little variation in adult size (Levi 1970). These data imply that the change in size at ecdysis is also plastic, fitting trajectory D, and that size at maturity may be constrained. Miyashita (1969, 1986, 1987) has documented plasticity in number of instars and intermolt duration in a variety of spiders, indicating that they may fit trajectory C or D. Polis and Sissom (1990) report that scorpions in general have an indeterminate number of juvenile instars, variable intermolt interval, and variable size at maturity related to variation in feeding history. However, they do not indicate whether the growth per ecdysis is variable or canalized, making it unclear whether these organisms fit trajectory C or D. In the mantid *Tenodera sinensis,* Paradise and Stamp (1991) report diet-dependent variation in the intermolt interval, growth per ecdysis, and the number of juvenile instars, implying a completely plastic trajectory D. They also report variation among sibling groups in the diet-dependent change in the intermolt interval. This implies genetic variation in the degree of plasticity. Recent experiments successfully selecting for changes in the degree of developmental response to diet in *Drosophila melanogaster* (Hillesheim and Stearns 1991) and past experiments examining plasticity in plants (Bradshaw 1965; Schlichting and Levin 1986) indicate that genetic variability in the degree of plasticity in developmental parameters may be widespread.

Genetic variation is also reported for the values at which canalized postembryonic developmental parameters are set. In *N. clavipes,* there is interpopulational variation in the growth per molt (Higgins 1992, 1993). In the butterfly *Euphydrias editha* and in the cricket *Allonemobious faciatus,* there is heritable interpopulational variation in adult size, implying that some canalized aspect of development varies genetically among populations (M. Singer pers. comm. 1993; Mousseau and Roff 1989). In several *Oncopeltus* species, there is reported to be heritable variation for size at maturity (Dingle et al. 1980). As the number of juvenile instars is apparently invariable, this implies genetic variation in min-

imum premolt weight. The constant number of juvenile stages in the genus *Oncopeltus* appears to be a phylogenetic constraint that does not vary within or among species within the lineage. Such phylogenetic constraints in development, implying low levels of genetic variation within a species for the parameter in question, will limit both phenotypic and evolutionary responses to environmental variation.

As presented earlier, there are eight possible combinations of plasticity and canalization in the three parameters that determine age and size at maturity in this model (number of juvenile instars, intermolt duration, change in size at ecdysis; Table 1). Of these eight, only four patterns were clearly represented in the literature. The remaining four raise interesting questions concerning the evolutionary consequences of canalization.

Two of the remaining four possibilities, X1 and X2, include the combination of canalized intermolt duration and canalized change in size at ecdysis. This combination is impossible because of the relationship of these parameters to juvenile weight. If change in size at ecdysis is fixed, then premolt weight is fixed. Animals gaining weight slowly take longer to reach the necessary weight, and intermolt duration must vary inversely with the rate of weight gain. Conversely, given that the rate of weight gain is variable, if intermolt duration is fixed, then the change in size at ecdysis must vary. This is because the organism cannot, by definition, wait to gain more weight and must molt when the intermolt period ends. The amount it grows at ecdysis will be positively correlated with what it weighs at the time of ecdysis.

The remaining two combinations, E and F, may be maladaptive. Fixing the number of instars and the change in size at ecdysis fixes size at maturity, and fixing the number of instars and the intermolt duration fixes the age at maturity. Partial canalization, or bounds, on these parameters set maximum age or minimum size at maturity. Fixed or bounded age or size at maturity could result in lower fitness relative to individuals expressing plasticity in these characters. If size at maturity is fixed, then total developmental time under poor environmental conditions may be so extended that, in a seasonal environment, successful reproduction is impossible. The end of the growing season will cut short development. If age at maturity is fixed, maturation by slow-growing individuals may occur at such a small size that reproduction is impossible or severely compromised by small size. In a variable environment, plasticity in both age and size at sexual maturity is evolutionarily advantageous relative to fixed values for either factor (Wise 1987).

These arguments are based on the data from a small number of species, and the insect data are biased toward pests. Additionally, we have purposefully ignored organisms with more complex life cycles such as aphids and parasites. Very small arthropods with very short generation times and parasites may be much more developmentally canalized. The bias toward outbreak species may be correlated with a bias toward species with more plastic developmental pathways. Outbreak species readily adapt to environmental circumstances, so investigating them increases the likelihood of finding phenotypic plasticity. Canalized pathways or narrower bounds might be found in species confined to specific habitats and tropical species experiencing less strong seasonality.

RESPONSE TO SEASONAL SHIFTS VARIES WITH THE DEVELOPMENTAL TRAJECTORY

Although all of the observed developmental pathways can yield environmentally induced responses in age and size at maturity, organisms on different developmental trajectories are not equally able to compensate for poor growing conditions in seasonal environments (Fig. 2). Compensation refers to the ability of a slow-growing organism to achieve fitness equivalent to conspecifics of the same population existing in better-quality microhabitats (Schmalhausen 1949, p. 185). Partial compensation is achieved if the slow-growing individual successfully reproduces but has reduced fitness compared with the fast-growing individual. To evaluate the fitness consequences of these different developmental trajectories, we model the ability of an organism of each trajectory to survive a seasonal shift. The end of the season is heralded by some environmental cue. Once the cue has been received, a pupal or maturation molt will be triggered for the next ecdysis cycle, within the constraints of the developmental pathway. We assume that in order to survive, the organism must either pupate (holometabolous) or mature (hemimetabolous) prior to the end of the season.

The restrictions placed on the developmental trajectories A, B, and E appear to prohibit very slow-growing individuals from achieving pupation or maturation by the end of the season. In the case of trajectory A, the critical factor appears to be the minimum size for pupation, not the maximum intermolt interval. Even if there were variation in the intermolt interval, the slow-growing individual is unlikely to achieve the minimum critical size for pupation (see the discussion of trajectory D, below). In trajectories B and E, the canalization in the number of molts makes it difficult for the slow-growing individual to respond to the cue for the end of the season: the individual must pass through the required number of stages. In all three cases, the restrictions in the development of the juveniles prohibit even partial compensation for the poor environments experienced. For species with these trajectories existing in strongly seasonal environments, other mechanisms of response to temporal changes are expected to have evolved, such as diapause or migration. In some groups juvenile diapause is postulated to have evolved in response to strong seasonality (e.g., *Meta mengei*; Toft 1983). If there is no diapause or migration, the geographic ranges of organisms with these developmental trajectories are necessarily restricted to less seasonal habitats. Several groups exhibiting trajectory B, such as *Oncopeltus* milkweed bugs and passalid beetles, are most diverse in less seasonal, tropical regions. This may reflect the lack of genetic or phenotypic variation for developmental responses to strong seasonal changes.

Plasticity in maturation size and number of juvenile instars allow individuals with developmental trajectories C and D to respond successfully to cues signaling the end of the season. When a slow-growing individual in trajectory C perceives end-of-season cues, it can mature in the next instar. Only if the necessary premolt weight is not achieved, prohibiting the molt, will this individual fail to mature. Plasticity in the number of juvenile molts and size at maturation also allow organisms in trajectory D to respond to the end-of-season cue and mature. In this case, the minimum size for
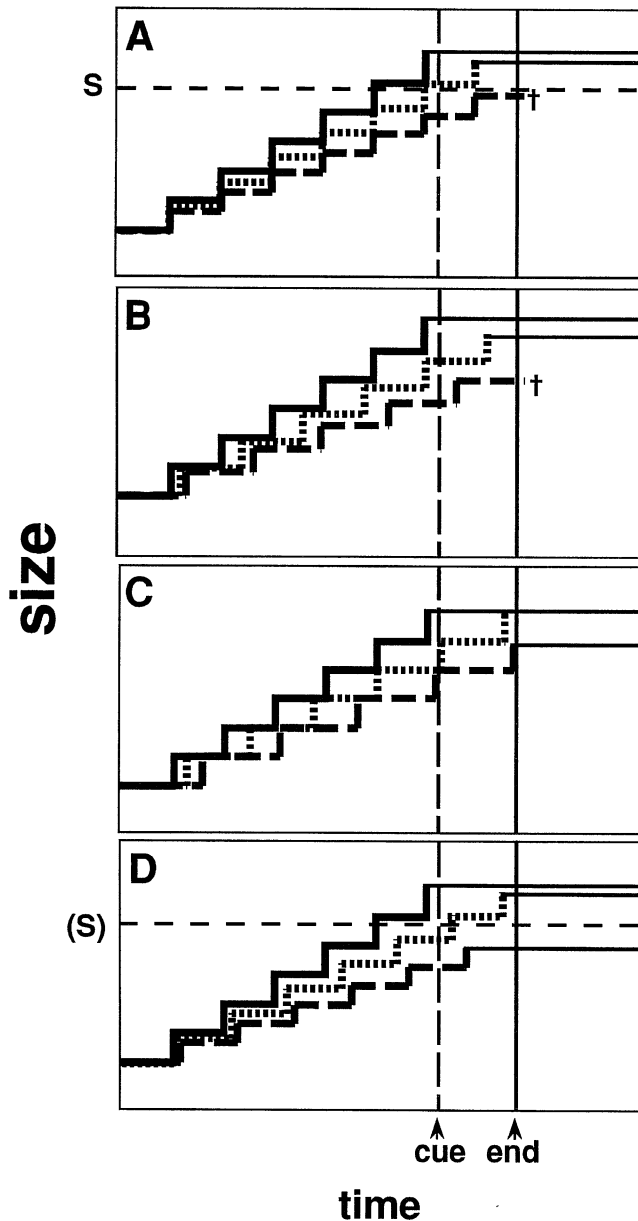
FIG. 2. The response to a cue heralding the end of the growing season will depend upon the type of developmental pathway. In each case, the heavy solid line represents the best growing conditions, the heavy dotted line represents intermediate conditions, and the heavy dashed line indicates poor conditions. The slope of the growth curve for a given condition is the same in all four illustrations. The end of the season is demarcated by the vertical solid line, and the cue heralding the end of the season by the vertical dashed line. † refers to death prior to maturation. (A) The presence of the minimum critical size for pupation, S, prohibits the most slow-growing individual from responding to the end-of-season cue. (B) The restricted number of juvenile stages prohibits the most slow-growing individual from responding to the end-of-season cue. (C) The variation in number of juvenile stages allows the most slow-growing individuals to respond to the end-of-season cue by maturing in the next molt, at a smaller instar than more rapidly growing individuals. (D) The absence of expression of the minimum critical size for pupation or maturation (S) will allow the most slow-growing individual to respond to the end-of-season cue by pupating (or maturing) in the next instar. If this canalization is expressed, then this individual will fail to reach the critical size and will not survive the end of the season.

maturation is indicated by a parenthetical S, as this is occasionally expressed. When the restriction of minimum size is present, then the slow-growing individual will fail to reach maturity, as in trajectory A. If not present, the slow-growing individual can mature or pupate at a much smaller size. Because slow-growing organisms with trajectories C and D achieve maturity at a smaller size and presumably have lower fecundity, there is only partial compensation by individuals experiencing poor growing conditions (e.g., Forrest 1987; Miyashita 1991; pers. obs.). However, they do reach maturity and therefore have a greater chance of reproduction than slowly growing organisms in trajectories A and B.

The actual fitness consequences of late maturation (extended generation time) and small size (lowered clutch size) will depend on the organism and the environmental seasonality. Because fertility is often a linear function of size in arthropods, if multiple generations per season are possible, the benefit of shortened generation time will outweigh the increased fecundity of greater size at maturity (Stearns 1992). If an organism is annual, with only one generation possible in each growing season, then increased developmental time that results in increased size at maturity can theoretically result in full compensation or even over compensation (greater fitness). However, increased developmental time in slowly growing individuals does not always result in larger individuals; late individuals may be smaller (Forrest 1987; Miyashita 1991; pers. obs.). The actual correlation between age and size at maturity under different environmental conditions will depend on which developmental parameters are plastic.

DISCUSSION

Although fully plastic developmental pathways might always be advantageous, the existence of a canalized parameter in most species suggests either an advantage of partial restrictions on development or inherent limits to plasticity. Under certain spatial and temporal scale of environmental variation, reflecting the reliability of the environmental cues (and the likelihood that cues would be properly interpreted) genetically variable developmental canalization could be advantageous. Canalization and maintenance of genetic variation for development is favored when environmental variation occurs among generations or over large distances (Stearns 1982; Gomulkiewicz and Kirkpatrick 1992), that is, when cues received by an individual are unreliable predictors of environmental quality during its life span. Developmental plasticity is favored when environmental variation occurs within generations, over small spatial scale (Stearns 1982; Gomulkiewicz and Kirkpatrick 1992) or other situations when cues are reliable.

Many questions about the physiological bases of developmental canalizations remain unanswered. There has been a lot of work done on the hormonal basis of molting and on the hormonal differences between molting to a juvenile stage and molting to either maturation or pupation (Beck 1971b, 1972; Nijhout and Williams 1974a,b; Blakley and Goodner 1978; Nijhout 1979, 1981; Safranek and Williams 1984b; Riddiford 1985). The decision of whether to molt to a juvenile instar or to a mature or pupal stage has been studied in *Manduca sexta* (Nijhout and Williams 1974a,b). Data from Ni-

jhout (1975, 1979) indicate that in *O. faciatus* the relative allometry of size and weight are important in turning on the hormones that initiate the molt cycle. However, except for Nijhout's work, the means by which an organism assesses its size and weight relative to environmental conditions are not well studied. Without a better understanding of how an individual assesses its internal and external situation, the physiological and biomechanical mechanisms of canalization cannot be fully understood.

Maxima or minima that constrain growth per ecdysis, premolt weight and intermolt duration may reflect mechanical or physiological limitations of the developmental processes in arthropods. A maximum growth per ecdysis is be expected for all organisms. The new cuticle must be packed within the old, and there is probably a limit to how tightly cuticle can be packed and how much expansion the new cuticle can undergo following ecdysis before sclerotization. A minimum premolt weight may reflect the nutritional requirements necessary to synthesize new cuticle. Organisms with juvenile retrogressive molts are sacrificing tissue to form the new cuticle. Even in these species, a minimum premolt weight must be met before pupation or maturation, presumably reflecting nutritional requirements for the major reorganization that occurs with metamorphosis and the energetic requirements for reproduction following maturation. Retrogressive or stationary molts reflect the existence of a maximum intermolt duration. This may be a physiological response to low environmental quality: if a juvenile is failing to gain weight, molting to a smaller size will reduce the nutritional requirements for maintenance. An interesting corollary is that in life cycles including dormant larval stages, the dormant stage is usually reached by a retrogressive molt.

Additionally, the evolution of developmental plasticity may sometimes be prevented by lack of genetic variation. Both developmental plasticity itself and the range of possible phenotypes are under genetic control (Schmalhausen 1949; Bradshaw 1965; Schlichting and Levin 1986; Hillesheim and Stearns 1991). For instance, in hemiptera it may be that there is no phenotypic variation in the number of larval stages because there is no genetic variation. If so, this aspect of development would be not only developmentally canalized but also evolutionarily constrained.

Most arthropods have some ability to respond phenotypically to their environment, and many are highly plastic. This has serious implications for traditional models of life-history evolution. The literature emphasizes age and size at maturity and deemphasizes underlying growth and developmental characters. This is true both of models that investigate life-history and empirical studies of life-history trade-offs. Most models of the evolution of complex life histories assume genetic determination of both age and size at maturation and examine the evolutionary optimization of reproductive capacity through changes in these parameters (e.g., Istock 1967; Gadgil and Bossert 1970). The emphasis on genetically determined traits may reflect the mathematical complexity of plasticity. Modeling the evolution of plasticity requires describing the evolution of a gene × environment interaction (Via and Lande 1985; de Jong 1990; Gomulkiewicz and Kirkpatrick 1992), which is intrinsically more difficult than mod-

eling either genetic or environmental variation alone (de Jong 1990).

Understanding the role of plasticity in the evolution of life histories of arthropods requires a better understanding of the processes of postembryonic development and experimental examination of the consequences of variation in the degree of plasticity. Perhaps foremost is the need to understand the physiological and genetic basis of canalization and plasticity. It is unclear whether the bounded parameters such as premolt weight reflect physiological necessity, and hence are evolutionarily constrained, or whether there may be genetic variation for these characters and how selection might operate on such variation.

Hillesheim and Stearns (1991) have shown that the degree of developmental plasticity can evolve under artificial selection, so experimental examination of the evolution of plasticity and canalization is feasible. If it is possible to select for combinations of canalization not usually found in nature (e.g., our trajectories E and F), it would imply that their rarity in nature reflects maladaptation rather than lack of genetic diversity. If alternative developmental pathways can be developed within a single species, competition experiments would show relative fitness of individuals with different degrees of canalized development. Using such systems, it should also be possible to test the predictions of the models of Gomulkiewicz and Kirkpatrick (1992) and Stearns (1982) concerning the role of the scale and predictability of environmental variation in the evolution of genetic versus phenotypic variation. The prevalence of phenotypic plasticity in many terrestrial arthropods makes it important to document in order the physiological basis of canalization and the ecological correlates of plasticity to understand the evolutionary consequences of development.

CONCLUSIONS

The developmental response by an individual to its environment will depend upon the existence of plasticity in postembryonic development and the manner in which the plasticity is expressed. The complex postembryonic developmental pathway of an arthropod is described by several interdependent parameters, some canalized and some plastic. When there is both spatial and temporal heterogeneity in the environment, the exact identity of the canalized parameters of development becomes particularly critical: despite cues of changing environmental quality, the organism may not be able to respond developmentally.

Examining only the end point of this complex process, the size or age at maturity under one versus another environmental condition, is similar to examining only the intrinsic rate of growth of a population. As demonstrated by Wade (1976), directional selection on this compound parameter can result in shifts in any one of a number of aspects of the biology: fecundity, cannibalism, or mortality. These distinct responses have very different biological implications. Likewise, selection for increased or decreased response to the environment, as measured by the amount of variation in adult size or adult age, could lead to a variety of changes within the developmental program that have very different biological implications. Only by distinguishing among the different

parameters, and examining each for a response to the environment, will it be possible to describe the evolution of growth curves and complex life histories.

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