



**Adaptive Plasticity and Plasticity as an Adaptation: A Selective Review of Plasticity in Animal Morphology and Life History**

Karl Gotthard; Sören Nylin

*Oikos*, Vol. 74, No. 1. (Oct., 1995), pp. 3-17.

Stable URL:

<http://links.jstor.org/sici?sici=0030-1299%28199510%2974%3A1%3C3%3AAPAPAA%3E2.0.CO%3B2-Q>

*Oikos* is currently published by Nordic Society Oikos.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/oikos.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## MINI- REVIEW

**Minireviews** provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

---

# Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history

Karl Gotthard and Sören Nylin

Gotthard, K. and Nylin, S. 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. – *Oikos* 74: 3–17.

During the last decade there has been a rapidly growing interest in the study of phenotypic plasticity in animals. Confused terminology in this field of research may be one reason why the focus of many studies is not as clear as it could be. The field of plasticity highlights the general problem of demonstrating adaptation. We discuss the terminology and methodology of plasticity studies, with particular reference to the question of which patterns should be considered evidence for plasticity as an adaptation to the environment, and how to find such evidence. We suggest a terminology where plasticity can be “adaptive” (i.e. beneficial, and maintained by selection) with respect to a function without strictly being an adaptation for it (evolutionary origin linked to this function), and vice versa. Modifications of the original reaction norm, seen today as differences in plasticity between populations and species, can be adaptations for a function even when the plasticity itself is not (it may follow from constraints or from selection for another function). We selectively review cases reported as evidence of adaptive plasticity in animal morphology and life history, choosing examples from a wide range of taxa to illustrate our criteria for what should be called “adaptive” and “adaptation” when applied to plasticity.

*K. Gotthard and S. Nylin, Dept of Zoology, Stockholm Univ., S-106 91 Stockholm, Sweden.*

“When a variation is of the slightest use to a being, we cannot tell how much of it to attribute to the accumulative action of natural selection, and how much to the conditions of life. Thus, it is well known to furriers that animals of the same species have thicker and better fur the more severe the climate is under which they have lived; but who can tell how much of this difference may be due to the warmest-clad individuals having been favoured and preserved during many generations, and how much to the direct action of the severe climate? for it would appear that climate has some direct action on the hair of our domestic quadrupeds.”

Charles Darwin (1859)

The variation of organic forms in nature have different sources (genetic and environmental), as exemplified by Darwin’s statement above. Although the interest for phenotypic plasticity has a relatively long history (Merrifield and Poulton 1899, Woltereck 1909, Schmalhausen 1949, Bradshaw 1965, Shapiro 1976), several reviewers mention the unpopularity of studying the evolution of environmentally dependent characters (Shapiro 1976, Schlichting 1986, West-Eberhart 1989). The reason for this relative lack of interest was probably that variation

---

Accepted 29 March 1995

Copyright © OIKOS 1995

ISSN 0030-1299

Printed in Denmark – all rights reserved

caused by environmental factors were considered non-heritable and consequently could not be altered by natural selection. However, it has long been known that genotypes can express different phenotypes, depending on the environment, and that some of the variation in this ability is heritable (Woltereck 1909). Bradshaw (1965), in his review of phenotypic plasticity in plants, concluded that the plasticity of a character appears to be specific for that character, specific in relation to particular environmental influences, specific in direction, under genetic control, and able to be radically altered by selection.

In the last decade interest in phenotypic plasticity in evolutionary biology has grown rapidly, especially in evolutionary ecology and genetics. This interest has resulted in both experimental and theoretical studies of plasticity in a wide range of taxa and traits, including morphological and life history characters (see e.g. Gupta and Lewontin 1982, Via and Lande 1985, 1987, Schlichting 1986, 1989, Stearns and Koella 1986, Sultan 1987, Nylin et al. 1989, Scharloo 1989, Stearns 1989, 1992, van Noordwijk 1989, West-Eberhart 1989, Wiklund et al. 1991, Negus and Berger 1992, Newman 1992, Scheiner 1993a, Windig 1993, Nylin 1994). Considering the large number of published studies and reviews of (presumably adaptive) phenotypic plasticity, remarkably little attention has been given to the question of what *is* adaptive plasticity. Besides brief comments on the subject, only Newman (1992) has specifically dealt with this question, in his important review of amphibian plasticity. However, his treatment is rather specific to the subject of plastic timing of metamorphosis. Also, for reasons discussed in detail below, we do not fully agree with his conclusions and suggested research methodology. In particular, there seems to be great confusion regarding how basic terminology in evolutionary biology should be applied to plasticity. What is "adaptive", and what is an "adaptation" in the case of plasticity; are they the same? Should the origin and maintenance of an "adaptive" feature be distinguished? If so, different methods are needed to deal with the two different questions. Confused terminology may be one reason why the focus of many studies is not as clear as it could be.

This review is divided into two sections. In the first, we introduce the concept of reaction norms, and use it to discuss phenotypic plasticity as a putative adaptation. The second part is a selective review of some empirical studies of possibly adaptive plasticity. We have selected the examples to illustrate different methods for demonstrating adaptive plasticity, and when plasticity can be considered an adaptation to a specific environmental heterogeneity. We have also, when possible, tried to use examples that have not been reviewed before.

## Phenotypic plasticity – principles

### Reaction norms

In the study of phenotypic plasticity, the most important theoretical tool, or descriptive model, is arguably the concept of reaction norms (Woltereck 1909, Schmalhausen 1949). It is a way of describing and visualising plasticity, and can be defined as "the set of phenotypes expressed by a single genotype across a range of environmental conditions" (Stearns et al. 1991). A reaction norm is consequently a property of a genotype (a clone or any category of genetically related individuals), summarising the direction and amount of plasticity that it is able to express. Differences between genotypes in this ability will result in different reaction norms, and to the extent that the reaction norms are heritable they will form the basis for evolution of phenotypic plasticity. Reaction norms are usually represented as a line or a curve on a graph that plots phenotypes against an environmental factor.

The exact genetic nature of reaction norms, and how they evolve, is rather controversial and has recently caused discussion (Scheiner 1993b, Schlichting and Pigliucci 1993, Via 1993a,b). Via and Lande have presented a model (based on quantitative genetics) of the evolution of irreversible phenotypic plasticity as a consequence of selection for different trait means in different environments (Via and Lande 1985, 1987, Via 1987). According to their model, adaptive reaction norms are merely by-products of selection on trait means within environments, rather than a result of selection for plasticity itself. There is therefore no need to invoke separate genes that control the shape of reaction norms (Via 1993a). This view has been challenged by others, who argue that there is evidence for the existence of plasticity genes, defined as environmentally dependent regulatory loci that control structural gene expression (Scheiner 1993b, Schlichting and Pigliucci 1993). Via (1993b) in a reply, agrees that "environment-specific control of gene expression by regulatory loci can play an important role in phenotypic plasticity".

We agree with Scheiner (1993b) and Schlichting and Pigliucci (1993) that genes for plasticity evidently exist, and plasticity itself can respond to selection (c.f. Scheiner and Lyman 1989, Hillesheim and Stearns 1991). The point made by Via (1993a) is important, however. A reaction norm should not uncritically be thought of as selected for per se, and especially not all parts of a reaction norm together, as a whole. Moreover, the evolution of reaction norms is likely to depend on the relative frequency of different environments and their relative influence on overall fitness (Houston and McNamara 1992, Kawecki and Stearns 1993). It may be the case that the capacity for plasticity (e.g. a system for photoperiodic control, or a machinery linking chemical cues from predators to an induced defence) is often selected for per se, whereas modifications of reaction norms that subse-

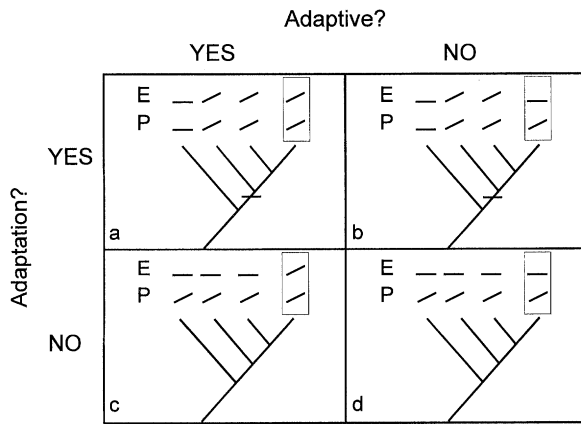


Fig. 1. The four possible combinations of the labels “adaptive” and “adaptation” that can be applied to a particular plasticity (reaction norm), and how they correspond to origin and maintenance of the plasticity by selection. The situations are illustrated by hypothetical phylogenetic evidence, where the studied species and its environment is indicated by a box. Plastic phenotypes (P), and changing environments (E) where this specific plasticity is adaptive with respect to a *specific function*, are both represented by sloping reaction norms. a) Plasticity which improves on a function in the present environment. The plasticity originated (at the point in the phylogeny indicated by a horizontal line) and is being maintained by selection for this function. b) Plasticity which improves on a function, but not in the present environment. The plasticity originated, but is not being maintained by selection for this function. It is present because of constraints on evolution or selection for a new function (not shown, E represents only the aspects of the environment which has relevance for the studied function). c) Plasticity which improves on a function in the present environment. It did not originate by selection for this function (it appeared before it was “adaptive” for this function), but is being maintained by it today. d) Plasticity which does not improve on a function. Such plasticity may follow from constraints (e.g. small size when food is scarce) or from selection for another function. Note that *differences* between genotypes in such “non-adaptive” plasticity may still be adaptive, and such modifications of the ancestral reaction norm can be adaptations (cf. Fig. 2).

quently evolve are often (but not always) the result of selection on trait means in different environments rather than on the whole reaction norm (e.g. on genes controlling the slope of a linear reaction norm). In the following discussion, we use the term “adaptation” to refer to the *modification* of the reaction norm, not to the entire new reaction norm.

## Adaptive plasticity and plasticity as an adaptation

### Adaptive and adaptation

To distinguish between adaptive and non-adaptive environmental effects is often not trivial. One genotype may mature at a small size when there is little food. This plasticity may be beneficial if it confers high fitness compared to genotypes that respond to low food levels by instead maturing later, or by dying. But is it an adaptation to varying food levels, or does it follow simply from

constraints? Such cases will be discussed more thoroughly below, but we see these specific problems as special cases of the more general question of defining “adaptation”, and how the term “adaptive” is related to “adaptation”.

There are at present two common uses of the term adaptive. Some authors use it as the adjective corresponding to “adaptation”, and equally restricted in its meaning. A trait can be beneficial, and as such possibly adaptive (i.e. a possible adaptation). It is adaptive for a function only if it can be shown that it is likely that it has arisen due to natural selection for this function. For other authors, “adaptive” for a function simply means beneficial for a function, as opposed to non-adaptive or even mal-adaptive traits. A beneficial trait is always adaptive, and possibly also an adaptation. Usually, it is not clear in exactly what meaning “adaptive” is being used.

The two meanings of the word easily become confused, because if a trait is obviously beneficial for a function, to the point that it seems designed for this function, it is also likely that it is an adaptation for this function. We propose, therefore, that it is best to explicitly distinguish adaptive (beneficial for a function) from adaptation (seemingly designed for a function, origin probably linked to this function). We find the distinction useful in separating the factors responsible for the maintenance of a trait from those responsible for its origin (Sultan 1987, Pagel 1994; cf. Fig. 1). A trait can then be adaptive with respect to a function without having originated due to natural selection for performing that function. Readers who do not want to compromise the meaning of “adaptive” can simply substitute it for “beneficial” in the following discussion and in Fig. 1.

### Adaptation: definition and methods

What, then, is an adaptation? This is a central question in evolutionary biology, and it has generated much discussion (c.f. Williams 1966, 1992, Curio 1973, Lewontin 1978, Wanntorp 1983, Stearns 1986, Coddington 1988, 1994, Pagel 1994). Most authors seem to agree on the basic notion that adaptations are products of natural selection that perform specific functions (Stearns 1986). Despite of this, different authors propose somewhat different, although not mutually exclusive, methods for testing adaptational hypotheses. In particular, the usefulness of comparative methods as opposed to theoretical modelling and subsequent experimental manipulation, for testing ideas about adaptations is somewhat controversial.

Williams (1992) argue that adaptations are features of organisms that conform to a priori design specifications. Examples that comes to mind are complex morphological traits seemingly designed to perform certain functions, but also behavioural or life history patterns that has quantitatively confirmed a priori optimality models. However, it should be stressed that there are severe problems (as Williams 1992, admits) in deciding when a trait conforms to design specifications. An extension of this view is the more pragmatic tradition to see beneficial for a function

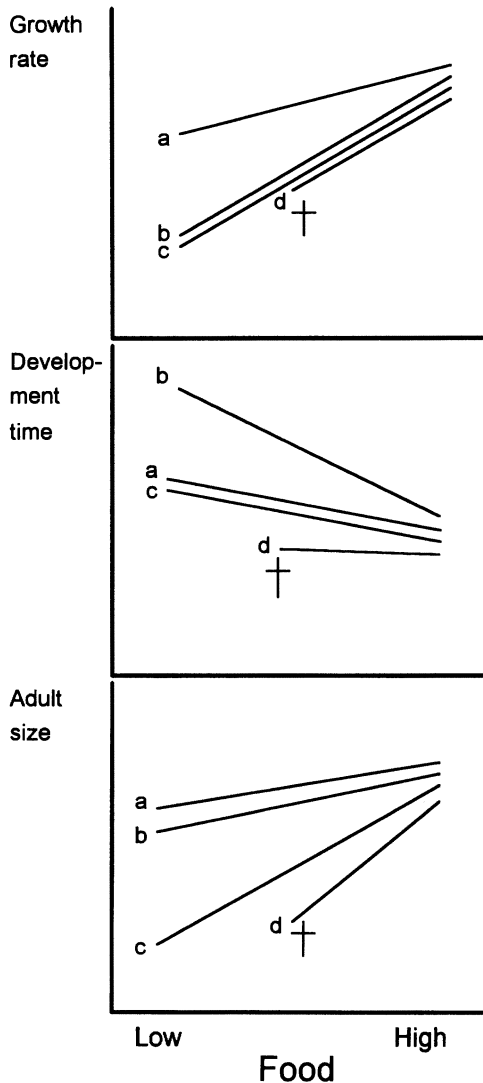


Fig. 2. A hypothetical comparison between four genotypes with different reaction norms for how three life history traits respond to a change in food abundance or quality. All genotypes perform equally at high food levels, for all three traits (the reaction norms have been spread slightly for clarity). Genotype a is best adapted to low food levels, as evidenced by the relatively high growth rates seen under such conditions. This means that it can sustain a relatively high adult size and still reach it in a relatively short time (compared to genotypes b and c). Genotypes b and c both show a life history plasticity which is better adapted to episodes of low food levels than genotype d, but their reaction norms represent alternative solutions to this problem. Genotype b responds by prolonging development time (reaching a size similar to genotype a). Genotype c instead matures at a small size, keeping development time relatively short (similar to genotype a). Genotype d has the most non-plastic development time, meaning that adult size rapidly decreases with decreasing food levels, and it does not survive to maturation at the lowest food levels. The differences between genotypes (which may also represent populations or species) may be local adaptations to the environment, if genotype a inhabits environments with varying food levels (low levels being common) whereas genotype d inhabits environments with constantly relatively high food levels, and the environments of b and c are intermediate.

as equal to adaptation for a function (cf. the previous section concerning the two meanings of “adaptive”). If a state is adaptive (beneficial), i.e. “fits the environment”, then it is also likely that the trait is an adaptation to that environment.

Another and more historically minded viewpoint is that adaptations are apomorphic (evolutionary derived) features that have evolved in response to natural (or any other kind of) selection for apomorphic functions (Wanntorp 1983, Coddington 1988, 1994, Brooks and McLennan 1991, Harvey and Pagel 1991, Pagel 1994). This definition is mainly concerned with adaptations at or above the species level, and stresses that only when a trait changes in response to a certain selective agent, to fulfil a certain function, can we call it an adaptation for that function. Consequently, in order to detect such a change it is necessary to have some knowledge of what the ancestral condition of the trait was, and this is possible by the use of comparative, especially phylogenetic methods.

As we see it, the design oriented methodology assumes that if a trait is beneficial for a function then it is likely that it has at least partly been shaped or modified by selection favouring individuals having this function, or it is at least being maintained by such selection today, because neutral or disadvantageous features are relatively quickly lost in evolution. If we use the historical methodology, on the other hand, claiming that a trait is shaped by selection in a certain environment means that we first have to rule out the possibility of it being present only for historical reasons. Thus, the central difference between these viewpoints seems largely to be due to how probable evolutionary change is considered to be, relative to the probability of stasis. In our opinion it is best to view the methods presented above not as competing but as complementary, logical frameworks for identifying likely adaptations.

Curio (1973) outlined a “research program” for identifying adaptations where he suggested comparisons between classes of organisms such as populations or species, and experimental manipulation of characters, as complementary methods. Throughout this paper we have tried to adopt this pragmatic approach, when discussing the evidence for or against the interpretation that a certain plastic response is a result of natural selection. For the scope of these discussions it is interesting that Curio (1973) mentioned plastic traits; i.e. traits that only appear in response to a stimulus in a situation where they increase fitness (but are not expressed or even reversed when the stimulus is not present or removed), as especially convincing cases of adaptation.

#### *Demonstrating adaptation: the problem with plasticity*

The field of phenotypic plasticity has its special problems in distinguishing adaptations, but at the same time plastic traits are often especially good for testing adaptational hypotheses. The problem arises from the fact that the expression of practically all traits is environmentally dependent, without necessarily being neither adaptive nor

adaptations. The good part is that it is often possible to experimentally alter the phenotypic expressions by manipulating the environmental parameter of interest, and to test whether the expression conforms to a priori predictions. The “design” criterion for recognising adaptations may often be of use, especially in the case of complex plasticity in morphology. Consider the case of protective spines induced in the presence of predators. The spines may be complex structures which, if they seem designed for protection against predators, are likely to be adaptations for this function. Note, however, that this does not necessarily mean that the plasticity per se is an adaptation. The fact that the spines are induced only in the presence of predators is better evidence that the plasticity really is designed for defence against predators which vary in occurrence. Life history plasticity is even more troublesome, because changes in size, development time and so on have potential to be caused by many factors, and to serve many functions. The environmental effect under study may be due to pure constraint, i.e. unavoidable physical or chemical processes. Plasticity in traits such as growth rates and number of offspring in response to temperature or food levels are examples where there are well developed, constraint, explanations. This type of plasticity may have an adaptive value without being a result of natural selection. Reaction norms in relation to food, population density and temperature are common in the literature which is not surprising given their importance as environmental factors (e.g. mammals: Albon et al. 1983, Jorgenson et al. 1993, Sæther and Heim 1993, Adler and Levins 1994; reptiles: Ford and Seigel 1989; amphibians: Newman 1989, 1992, Blouin 1992, Bernardo 1994; insects: Dingle 1992, Windig 1994; fish: Reznick and Yang 1993).

Newman (1992) recognised the problem of plasticity following simply from constraints and characterised plasticity of this type as “spandrels” (sensu Gould and Lewontin 1979) and not adaptations per se (cf. Fig. 1). In a further discussion of the temperature-dependence of amphibian development he pointed out that, “sensitivity to temperature (or any other factor) can be modified by natural selection (Huey and Kingsolver 1989), so tadpoles from habitats with variable pond duration may be more sensitive to an increase in temperature than tadpoles from other habitats”. Hence, although there are basic physical and chemical constraints (which partly are results of evolution past) on, for example, temperature or food level reaction norms, we should expect them to be modified by natural selection and such modifications would be adaptations to the specific temperature or food regimes in question. In some contrast to Newman (1992), we argue that reaction norm modifications of this kind are best revealed by comparative methods (cf. Fig. 2). It is often possible to predict how reaction norms between categories of organisms should differ, if the type of reaction norm modifications described above has occurred. The predictions may subsequently be experimentally tested by manipulation of the environmental factor of

interest. Here, we include comparisons between species, between populations within species, and even comparisons between genotypes within populations, among the comparative methods that can address the question of adaptation (cf. Curio 1973). Newman (1992) states that comparative studies of reaction norms in respect to habitat are “a useful starting point” for developing hypotheses about adaptive plasticity. Subsequent tests of claims about the adaptive nature of a response to environmental factors, especially those with non-adaptive alternative explanations must, according to Newman, “be based on measurement of fitness components”. We disagree with the view of comparative analysis as a “starting point” and as an inferior (Williams 1992) way to demonstrate adaptation. We see the two approaches as strictly complementary: they are alternative ways to demonstrate adaptation, but vary in usefulness depending on the studied trait. A combination of the two is often the most convincing for a complete demonstration of adaptation.

The strength of this combined approach is evident in a study by Berven et al. (1979), addressing plasticity in several life history variables of the green frog, *Rana clamitans*, in relation to temperature. The authors compared several populations of frogs from different altitudes and concluded that rearing temperature affected growth and development severely, independent of altitudinal origin. However, the exact nature of this temperature dependence differed between lowland and mountain populations. The duration of the larval period are probably closely related to fitness (Berven et al. 1979), which together with the known differences in temperature at high and low elevations would predict a reaction norm difference close to the observed. Thus, the comparison revealed that the reaction norms or at least parts of them are likely adaptations to different, specific distributions of temperatures.

#### *A summary of methods*

In summary and conclusion of this part of the paper, we distinguish between four possible combinations of the labels “adaptive” and “adaptation” that can be applied to a reaction norm or a plastic trait (Fig. 1). Neutral or negative direct effects of the environment (e.g. food, temperature) are neither adaptive nor adaptations. A predictable difference between genetic categories (e.g. sexes, populations, species) in such effects may however show that the reaction norm has been modified by selection in a way consistent with adaptation (cf. Fig. 2). Some plastic responses are clearly adaptations even though they may be maladaptive at least occasionally, e.g. when an animal changes to a white fur or plumage for crypsis in winter but it happens to be a year without snow. This might seem to be a trivial case of a too short time-span for the study (the plasticity is supposedly adaptive if fitness is measured over several years), but the example illustrates that there are many cases when we can be reasonably sure that a trait is an adaptation even though we may have trouble demonstrating that it is adaptive (cf.

Table 1. A summary of methods for demonstrating that an observed plasticity is adaptive, and demonstrating that it is a likely adaptation. Additional references are given in the text.

Evidence for	Examples
<b>Adaptive plasticity</b>	
Type of evidence:	
1. Optimality models predicting the reaction norm, followed by tests	Age and size at maturity (Stearns and Koella 1986, Sibly and Atkinson 1994)
2. Reciprocal experiments	Seasonal morphs in butterflies (Shapiro 1976)
<b>Adaptation within species</b>	
Type of evidence:	
1. Hypothesis based on optimality, predicting variation among populations, followed by tests	Growth rate in Atlantic silversides (Canover and Present 1990)
2. Reciprocal transplantations	Growth rate in <i>Sceloporus</i> lizards (Niewiarowski and Roosenburgh 1993)
<b>Adaptations at or above species level</b>	
Type of evidence:	
3. Phylogenetic methods	Wing polymorphism in water striders (Andersen 1993)
4. Species comparisons	Growth rate plasticity in voles (Negus and Berger 1992)
5. Design criterion	Fighting or cannibalistic morphs in response to density (e.g. Collins and Cheek 1983, Timms et al. 1981) Photoperiodism (e.g. Saunders 1982) Changes in morphology or life history induced by cues from predators (e.g. Brönmark and Miner 1992, Crowl and Covich 1990)

Williams 1992). Also, in some cases the adaptation may in fact not be adaptive at all in the present environment. It seems likely that ancestral reaction norms, or parts of reaction norms, which no longer serve a purpose are often present because of constraints on their evolution. A contributing factor could be that such "useless" reaction norms may carry few costs, if they are adaptations to environments which are no longer experienced. Finally, of course, there are many examples of plasticity which merit both labels, and some of them will be mentioned in the review section.

We suggest that it can be inferred or demonstrated in basically two ways that a reaction norm is adaptive (see Table 1):

1) By predicting the general shape of the reaction norm from verbal or mathematical optimality models, describing how different phenotypes should be related to environmental variables and how this would affect fitness components, and to show that the reaction norm agrees with predictions (Newman 1992).

2) By performing an experiment where the plastic genotype is demonstrated to have higher fitness than a non-plastic genotype, or a genotype with a different type of plasticity. One example is to demonstrate by manipulation that the different phenotypes produced by a plastic genotype have higher fitness than the alternative phenotype, in the respective environments where they are

presumably adaptive ("reciprocal experiments" in Table 1), e.g. demonstrate that a summer morph has higher fitness than a winter morph in summer and vice versa (Shapiro 1976).

In considering how to demonstrate that a trait is an adaptation, we distinguish between adaptations below the level of species and adaptations at or above this level (Table 1). The reason for this distinction is purely practical, phylogenetic techniques are seldom applied within species, where horizontal gene transfer is more common and obscures the phylogeny of populations. The differences between populations within a species represent variation which has been relatively rapidly accumulated since there was one single ancestral population, and if this variation is adaptive (beneficial at each locality, as inferred from models or demonstrated by experiments) this is most likely due to local modifications by selection. Evolutionary constraints probably have a very minor role in explaining the *differences* between populations in a trait varying in a quantitative manner. In the same way as for convergent modifications of quantitative species traits, we consider such "micro-apomorphies" (Nylin 1991) evidence of adaptation, if they are predictable and either complex enough or numerous enough to be unlikely to have arisen by chance. Population is the most commonly used genetic category for investigating plasticity in this comparative manner and here we will only

discuss such cases. In principle the same logic can be extended to other genetic classes within species, for instance to predictable differences in plasticity between sexes (Leimar et al. 1994). Demonstrating that reaction norm differences between genetic categories within species are likely adaptations for specific functions, can be done:

1) By optimality models predicting variation in reaction norms between for example populations followed by some type of test of correlation with environmental variables in the field. In the case of plasticity this is not entirely straightforward, because models and tests will have to be explicitly concerned with how the environment and the phenotype vary within as well as between populations. For one thing, the number of measurements needed to establish differences in reaction norms rapidly increases with the number of environments and populations included in the study. Literature data can seldom be used, because of the need for strictly controlled environments.

2) By experiments, where genotypes from each site are transferred and demonstrated to have the highest fitness at their own site of origin ("reciprocal transplantations" in Table 1). As mentioned, comparisons between genotypes within populations could be used as evidence of adaptation in a similar manner, if there is independent evidence that genotypes are associated with particular habitats, and reaction norms can be predicted to be associated with these habitats.

To demonstrate adaptation at or above the species level, phylogenetic methods are often useful. We distinguish between (cf. above):

3) Phylogenetic, comparative methods of various sorts. For example, a trait (in this case plasticity) can be studied as a synapomorphy, a historical unique, which is demonstrated to fulfil a function and where it is shown that it is likely that the plasticity arose because of selection favouring individuals that could perform this function (or improve on this function) (Coddington 1994). Such methods are most applicable to qualitative traits such as the presence/absence of a certain type of plasticity. Another class of comparative methods where phylogenies are used are the so called "contrast" methods (Felsenstein 1985, Harvey and Pagel 1991, Pagel 1994). These are used to test whether evolutionarily convergent, quantitative, modifications in a trait (in this case a reaction norm) are correlated with modifications in another trait or with an environmental variable, across species but controlling for phylogeny (Pagel 1994).

4) As explained above for population comparisons, there are practical problems in applying the "contrasts" type of test on quantitative variation in reaction norms. Usually, instead only a couple of species are compared, in a less rigorous manner. We will call this a "species comparison" (Table 1), and as phylogenies are not used, methods are very similar to those for demonstrating local adaptation of populations within species.

5) There are at least two different aspects of the ques-

tion of whether a reaction norm is seemingly designed for a function. First, do the *phenotypes* expressed by a reaction norm conform to a priori design criteria for performing a specific function? Second, is the *mechanism* for the induction of different phenotypes in different environments seemingly designed? Examples of the first statement may be conspicuous changes in morphology, where the morphologies can be predicted from design specifications or at least are shown to enhance fitness when performing a specific function. It is, nevertheless, the second aspect of the induction mechanism that offers the perhaps best evidence of whether a reaction norm is an adaptation using the design criterion. That is, when an environmentally induced phenotypic change is non-intuitive and we have no strong alternative explanations for it (as we do in the case of unspecific and direct effects of the environment on physiology) or when the phenotypic change actually occurs in response to a cue predicting future conditions, the design criterion could be applied. For example, a period of low activity in an insect which is directly caused by low temperature is not necessarily an adaptation to survive low temperatures, or delay reproduction until a more favourable time. In contrast, a dormancy which is induced by photoperiod, *before* the onset of unfavourable conditions (i.e. a diapause), is probably an adaptation for one or both of these functions. A change in life history or morphology in the presence of predators or parasites can be ambiguous as an adaptation, for instance because it may be a non-adaptive effect of changes in local competition. The change may even be induced by the predator/parasite for its own needs. If the change occurs in response to a long-distance chemical cue, which is released when conspecifics are wounded or eaten, there is stronger evidence that the plasticity is an adaptation for defence.

This argument must, however, be used in a relative manner. Small size in response to high density of conspecifics or low food levels is, for instance, more ambiguous as an adaptation than the development of teeth and a cannibalistic lifestyle as a response to the same environmental variables (Collins and Cheek 1983, Walls et al. 1993a,b). The design criterion can thus be invoked when the link between environment and phenotypic change is predictable, but improbable enough that it must have been shaped by selection. A combination of some element of design in the phenotypes (e.g. white colour in winter, brown in summer) and another element of design in the induction mechanism (e.g. photoperiodic control of colour change) is even more convincing.

## Phenotypic plasticity in animal life history and morphology – review

In this part of the paper we will review cases of presumably adaptive plasticity by investigating what type of evidence has been used, and in doing so try to fit them



into the structure of methods that we outlined in the preceding section (summary of methods, Table 1). Basically the review follows the same structure and we start by looking at cases where the plasticity is adaptive but not obvious adaptations and go on to cases where there is additional evidence that the plasticity in question has been shaped or altered by natural selection in a specified environment.

## Adaptive plasticity

### *Optimality models predicting the reaction norm, followed by test*

In an influential article Stearns and Koella (1986) presented optimality models for predicting reaction norms for age and size at maturity, and tested the models using data mainly from fish. Literature data were in good agreement with the model. Basically it explores how the optimal age and size at maturity may change, when growth rate varies as a function of the quality of the environment. This represents one of the first examples of the still rather few attempts to predict animal life history plasticity and the exact shape of reaction norms. Stearns and Koella's (1986) approach has been criticised, however, on the grounds that their models assume that offspring encounter the same environment as their parents (Houston and McNamara 1992, Kawecki and Stearns 1993). The essence of an optimal reaction norm should instead reflect the optimal evolutionary response to a range of environmental conditions that offspring may meet.

Amphibian life history and metamorphosis is an area of research that has produced some of the most interesting and intriguing studies of adaptive plasticity (reviewed by Newman 1992). Many studies have dealt with adaptive plasticity in life histories displayed by frogs, toads and salamanders that breed and grow as larvae in temporary ponds of often unpredictable duration (Semlitsch and Gibbons 1985, Petranksa and Sih 1987, Newman 1988a,b, 1989, Semlitsch and Wilbur 1988, Crump 1989, Semlitsch et al. 1990, Blouin 1992, Semlitsch 1993a, Bernardo 1994, Tejedo and Reques 1994). When a pond dries out the larvae in it are exposed to a high risk of mortality (Newman 1992). A general prediction in these studies is that it would be adaptive for larvae in ponds of variable duration to metamorphose early in ponds of short duration but delay metamorphosis in ponds of a longer duration. This prediction is also met in both field studies and when pond duration is experimentally manipulated. However, the disappearance of water is correlated with changes in other important environmental parameters such as abundance, food level and temperature. Thus, it is possible that the shorter larval times in ponds of shorter duration is just a consequence of higher temperatures in such ponds (Newman 1989, 1992). It seems likely that temperature affects larval growth in some way, and this may have an adaptive value but it is not clear from this that we can conclude that the plasticity is an adaptation to a certain distribution of pond duration times. To obtain

more evidence for interpreting these reaction norms as adaptations it is possible to do comparative studies of reaction norms between populations and/or species, predicting how populations or species should differ, based on knowledge of their habitats (Semlitsch et al. 1990, Blouin 1992, Semlitsch 1993a, Bernardo 1994).

The general response of ectothermic animals to higher temperatures during juvenile development seems to be a higher growth rate, leading to a short development time but also to a smaller size at maturity (reviewed in Atkinson 1994, Sibly and Atkinson 1994). This is usually only true for temperatures within certain limits, and stressful temperatures above these limits often have the effect to reduce growth rate (Berven et al. 1979, Conover and Present 1990, Meffe 1992). With some basic knowledge of temperature dependence of biochemical reactions the outlined effect on growth rate and development time is not surprising. However, that an increase in growth rate should lead to a smaller size at maturity is non-intuitive and this type of response has in fact turned out to be very difficult to predict using models for the evolution of age and size at maturity (Sibly and Atkinson 1994, Berrigan and Charnov 1994). Addressing this problem, Sibly and Atkinson (1994) presented a model of optimal age and size at maturity in ectotherms in relation to variation in rearing temperature, that under certain conditions could generate such a prediction. An important point is that the observed variation in size at maturity is modelled as an adaptive response to changes in selection pressures associated with variation in temperature (Sibly and Atkinson 1994). Interestingly, there seems to be no causal relationship between a low growth rate and maturing at a large size per se, because when growth rate is lowered by decreasing the food quality ectotherms typically delay maturation and mature at a *smaller* size (Berrigan and Charnov 1994). Thus, although low temperatures and low food quality affects growth rate similarly, the most common effect of those factors on adult body size is totally opposite of each other.

Food availability and quality are other environmental factors that we expect to affect life history traits, independent of whether these effects have been altered or caused by natural selection in a specified environment. Ford and Seigel (1989), investigated plasticity in relation to food level in the chequered garter snake, *Thamnophis marciianus*. On adaptive grounds they predicted that clutch mass and clutch size should be considerably plastic in response to food regime, while the relative clutch mass and offspring size should show little or no plasticity. The predictions were tested in a controlled experiment and found valid. The authors are nevertheless very careful in stating that they do not view these results as sufficient evidence to assume that the differences in plasticity among life history traits is a result of natural selection in the population in question. To throw some light on this question, it would perhaps be possible to compare the presence and nature of these reaction norms among populations with known differences in food availability that

could generate clear predictions, or use the between-species variation that seems to be present within the reptiles (Ford and Seigel 1989).

Reznick and Yang (1993), in a similar study of allocation to reproduction in female guppies (*Poecilia reticulata*), showed that females responded to low food levels by producing fewer but heavier offspring. The increase in weight was mainly due to larger fat reserves that can be used by offspring to survive a period of food shortage, indicating that the plastic allocation pattern may be an adaptation to varying food levels. However, Reznick and Yang (1993), argues that further investigation of this plasticity is needed to test if it is adaptive (our terminology). They suggest an experiment, where the offspring of low and high food females are put in either high or low food treatments and compared in terms of fitness. If the plasticity is adaptive, the larger offspring of low food females should have higher fitness in the low food treatment than the offspring of high food females (Reznick and Yang 1993). This type of experiment would fall in to the “reciprocal experiment” category (Table 1, next section).

#### *Reciprocal experiments*

The logic behind this method is rather clear-cut. If we can show that the different phenotypes which a reaction norm expresses all have higher fitness than any alternative phenotype (along the same reaction norm), in the environment where they are induced, then the reaction norm is adaptive. Scharloo (1989) reviewed some instances of possible adaptive plasticity in *Drosophila* where reciprocal experiments had been used to establish the adaptiveness of reaction norms. The methodology has also been used in investigating the significance of seasonal morphs in insects (Shapiro 1976, Saunders 1982). Although the phenomenon is present in many insect groups, it is most extensively studied in butterflies (Shapiro 1976). Adaptive explanations that have been suggested for butterfly seasonal polyphenism are seasonal variation in the need for thermoregulation (Watt 1968, 1969) and crypsis (Wiklund 1975, Brakefield and Larsen 1984, Brakefield and Reitsma 1991).

Wiklund (1975) monitored survival of differently coloured pupae of *Papilio machaon* in summer and winter, and found support for the crypsis function in summer (but not in winter). In pierid butterflies a common form of plasticity is that adults are darker in generations occurring during the cooler parts of the flight season. Shapiro (1976) released the respective morphs at the “right” and “wrong” times of the year and monitored survival. The results of these studies supported the adaptive function of the pigment for thermoregulation, and so do comparisons within and between species (Shapiro 1984). Shapiro’s summary of results from these studies (1984) is in line with our view as presented here: “... the thermoregulatory advantage is not yet proven ... though strongly suspected ... Whatever the adaptive significance of these patterns, there is compelling evidence that *they are adap-*

*tive*” (italics in original). In our terminology, we would say that it seems relatively clear from the photoperiodic regulation (seemingly “designed” mechanism) and from comparative patterns that the seasonal polyphenism in pierids represents adaptations to seasonal change, but it is not yet entirely clear what aspects of seasonal change they are adapted to. In most other cases the function is even less understood, such as the striking examples of polyphenism in *Araschnia*, *Precis* and *Polygonia* butterflies (see e.g. Shapiro 1976, Brakefield and Larsen 1984). It cannot be ruled out that some of these polyphenisms may lack function, either because the function has been lost, or because the polyphenism is in fact only an incidental effect of other differences between generations. For instance, differences in pupal development time may affect the ontogeny of wing pigmentation, and these effects may or may not be adaptations per se.

#### **Plasticity as an adaptation**

*Adaptations within species – Hypothesis based on optimality, predicting variation between populations, followed by tests*

The method of comparing population reaction norms has been used relatively frequently and has substantially increased the understanding of phenotypic plasticity as an adaptation. Conover and Present (1990) for example, reported a study on plasticity in growth rate in Atlantic silversides (*Menidia menidia*). They showed that, as expected from the south-north decline in the length of the growing season and the fact that body size was similar in all the studied populations, fish from northern populations grew faster than fish from southern populations. However, growth rate depended on temperature. Moreover, the reaction norms relating growth rate to temperature differed between populations. At low temperatures growth rates were similar, but at high temperatures fish from northern populations grew faster. Conover and Present (1990) concluded that, because large body size is important for winter survival, fish from high latitudes are adapted for rapid elevation of growth rate during the brief interval of the year when high temperatures occur.

Photoperiodism and seasonal plasticity in insects are areas of research that have a long tradition in doing population comparisons (Danilevskii 1965, Bradshaw 1976, 1990, Masaki 1978, Nylin et al. in press). Because of the strong correlation between seasonality, latitude and altitude, geographical “clines” in seasonal adaptations are a common phenomenon (Danilevskii 1965, Bradshaw 1976, 1990, Masaki 1978, Roff 1980 1983, Tauber et al. 1986, Nylin and Svård 1990, Nylin et al. in press). A typical within-species latitudinal pattern for an insect living in temperate climates is that the further north they live, the longer is the photoperiod that induces diapause. There is little doubt, that plasticity in response to photoperiod in general is an adaptation to seasonality (see later discussion of “design criteria”). However, population comparisons may be necessary to reveal if natural selec-

tion has finely tuned this general mechanism differently at different locations.

A case where a population comparison would be the obvious method to test the adaptational hypothesis is reported in a study of temperature reaction norms in eastern mosquito fish, *Gambusia holbrooki* (Meffe 1992). The temperature dependence of growth, age and size at maturity of this species was studied in a population that had been exposed to abnormally high temperatures during approximately 28 yr, due to emission of cooling water from a nuclear power plant. The results indicate that fish from this population grow slower but mature earlier at smaller sizes in high, stressful temperatures compared to low temperatures. This plasticity is different to what is known from other related fish species and it is perhaps adaptive (Meffe 1992, and references therein). However, a comparison between this and neighbour populations of *G. holbrooki*, would probably be the best way to resolve whether the observed response to temperature is in fact species-specific (at the most a pre-adaptation to power plants and other sources of high temperatures), or due to local adaptation to periods of high water temperatures. The comparisons with other related species cited above will help to establish the ancestral reaction norm for the species in a subsequent phylogenetic analysis.

Madsen and Shine (1993) studied the plasticity in body size in two populations of grass snakes (*Natrix natrix*) in response to food availability. They wanted to test whether the differences in average female size was due to genetic differences between the populations or just caused by the fact that the prey available on the island were of poorer quality. This was done by rearing mainland- and island snakes in captivity under food conditions similar to what the mainland populations experience in the wild, and the results showed no difference in growth rate or final size between the populations. From this the authors suggest that the populations share a single norm of reaction, which may well be true. However, we do not think it is possible to conclude it from this study alone. Madsen and Shine have shown that the reaction norms of the populations do not differ at a certain point, the high food level (mainland diet). There may nevertheless be differences at other points on the reaction norms, of which the food level equal to the island diet is one (cf. Fig. 2).

For the sake of explaining the method of comparing population level reaction norms it is interesting to compare the last two studies (Meffe 1992, Madsen and Shine 1993), although, in our opinion, none of them have explicitly tested whether the plasticity in each case really are adaptations. In one case (mosquitofish; Meffe 1992), the presumably adaptive variation in reaction norms *between populations* has not been thoroughly explored. In the other case (grass snakes; Madsen and Shine 1993), the possibility of adaptive variation in body size *between environments* (food regimes) has not been investigated in full. The essence of the method is, however, to use both components of variation, within and between populations, to test hypotheses about adaptation.

#### *Adaptations within species – Reciprocal transplantations*

Compared to laboratory experiments (see the preceding section), reciprocal transplantations have very rarely been used for testing hypotheses about phenotypic plasticity as a local adaptation in animals. This is perhaps not surprising, considering the logistic problems of transplanting animals from one site to another and, furthermore, to keep track of them afterwards. Nevertheless, Niewiarowski and Roosenburg (1993) used this method to study the environmental dependence of growth rates in fence lizards, *Sceloporus undulatus*. They discovered a genetically based difference between populations of this lizard in how the environment affected growth rate, by transplanting lizards from New Jersey to Nebraska and vice versa. The lizards from Nebraska and other western grasslands apparently grow at a rate 2–3 times higher than the eastern woodland populations (Jones and Ballinger 1987, Niewiarowski and Roosenburg 1993). However, when Nebraskan lizards were held in enclosures in New Jersey they did not grow faster than the residents. The lizards from New Jersey on the other hand kept their low growth rate when moved to Nebraska. The daily potential activity period experienced by lizards in New Jersey was 2–2.5 h shorter than in Nebraska, and the authors argue that this is a possible selective force that could be responsible for the differences observed.

The strength of this type of experiment is of course that it is done in the field, and that the population comparison therefore is more likely to reveal evolutionary and ecologically important differences between populations. The main problem, however, is that unless we use controlled laboratory environments it is difficult to identify the specific aspect/aspects of the environment to which the plasticity is a potential adaptation. A combination of laboratory experiments and reciprocal transplantations would probably give very convincing arguments for or against adaptational hypotheses.

#### *Phylogenetic methods*

Comparative studies of plasticity at the species level are very rare. The only study of phenotypic plasticity where phylogenies have been explicitly used is, as far as we know, the case of wing polymorphism in water striders (Gerridae) (Andersen 1993). Water striders inhabit various types of fresh and brackish water bodies variable in space and time. The habitats include both highly predictable permanent waters and unpredictable temporal rock pools (Väpsäläinen 1978, Kaitala 1987, 1991, Andersen 1993). In several cases the variation in life history, wing length and wing muscles is a result of phenotypic plasticity, but not always. Väpsäläinen (1978) suggested a correlation between wing polymorphism (genetic and permanent, or seasonal and plastic) and the permanency of the habitat among water striders, and Andersen (1993) performed a phylogenetic analysis of such patterns. He concluded that wing polymorphism and/or a monomorphic short-winged state is ancestral for the studied taxa,

whereas a monomorphic long-winged state has evolved in species inhabiting waters of short duration. In other words, plasticity in wing length evolved early in the evolution of water striders (an adaptation at a high taxonomic level) but has sometimes been lost (adaptations closer to the species level). The relationship between genetically and environmentally determined polymorphism among and within species is unclear, as is often the case in similar systems. We suggest that this is to be expected, because there is often genetic variation in reaction norms. If variation persists in the shape and/or level of the reaction norms we will perceive this as a mixture of genetic and environmentally determined variation. Systems where the relationship between genetic determination and plasticity is unclear should in fact be prime targets for research to clarify how plasticity is selected, because in such systems it is likely that genetic variation in reaction norms will be found.

#### *Species comparisons*

As mentioned earlier there are severe logistic problems associated with extensive comparative studies of reaction norms that varies quantitatively. This together with the fact that reliable phylogenies still often are absent, may explain why such studies have not yet been published. Nevertheless, there are some examples where researchers have inferred a reaction norm to be a possible adaptation, by comparing just a few species and relating any reaction norm differences between them to differences in their ecology or environment.

Blouin (1992) measured time and size at metamorphosis in relation to temperature in three species of frogs in the genus *Hyla*. He then constructed "species"-reaction norms and made comparisons between them in relation to differences in larval habitats among the species. All three species developed faster in higher temperatures, but it was only in one of the species, *H. squirella*, that this faster development did not result in a smaller size at metamorphosis. Since this was the species that had the most ephemeral larval habitat, the differences in the reaction norm relating temperature to age and size at metamorphosis may reflect different selection pressures. Although the results in this particular case are not conclusive, they show that the environmental dependence of life history traits may differ between species, and that it may do so in a predictable manner.

A mammalian example of possibly adaptive plasticity in life history traits is reported from mountain voles, *Microtus montanus*, in North America. The voles exhibit slow growth rates and delay sexual maturation when they are facing drought-induced deterioration of food (Negus and Berger 1992). The observed change in life history seemed not to be just a direct consequence of food shortage, because the animals were in excellent condition and were not suffering from starvation. In other words, growth seemed to be slow in response to the lack of rainfall *predicting* food shortage. Negus and Berger (1992) suggest that other vole species should be exam-

ined, apparently in an attempt to test for adaptation at the species level or above by comparative methods. They note that *M. longicaudus*, which is characterised by more stable population dynamics, does not appear to show plasticity of growth patterns. This single contrast supports the hypothesis of adaptation, and another strategy could be to examine similar contrasts in more distantly related taxa to obtain evidence for or against convergent evolution.

#### *Design criterion*

An example where adaptation can be inferred using the design argument is the plasticity in response to population density found in the acarid mite, *Caloglyphus berlesei*. Males of this species develop into a "fighter"-morph in small colonies and to a "non-fighter"-morph in dense populations (Timms et al. 1981). The fighters have one pair of modified legs that is thickened and sharply terminated and is used to kill other males. Radwan (1993), furthermore, showed that reproductive success was higher for fighters in small colonies but lower in dense populations, compared to non-fighters. The reason for this was that in small colonies a single fighter male often killed all other males and monopolised the females, but in large colonies the fighters were killed in fights more often than non-fighters. Fights are probably also costly in terms of time and energy. Thus, the "adaptive" nature of this plasticity can be inferred using the "optimality" approach (Radwan 1993). In addition, this plasticity is very probably an adaptation, because of the seemingly designed "killer legs" and the indirect nature of the induction mechanism. It does not seem plausible that population density would have this particular effect on morphology, unless the link between cause and effect has been selected for.

An area where several instances of adaptive morphological plasticity have been identified, implicitly by the use of the design criterion, is the phenomena of predator-induced defences (reviewed by Dodson 1989 and Adler and Harvell 1990). Well known cases that have been thoroughly investigated are the induction of protective structures in several species of *Daphnia* (c.f. Dodson 1989, Riessen and Sprules 1990, Parejeko and Dodson 1991, Lüning 1994), rotifers (c.f. Gilbert 1980, Stemberger and Gilbert 1987) and bryozoans (c.f. Adler and Harvell 1990, Harvell and Helling 1993). In all of these and in several other instances mentioned in the reviews above, the morphological changes are induced by water-borne chemicals released by the action of predators. There are also examples of adaptive life history plasticity in response to such chemicals (cf. Crowl and Covich 1990). The first example of a predator-induced reaction norm in a vertebrate is reported by Brönmark and Miner (1992). They studied how body morphology in a freshwater fish, crucian carp (*Carassius carassius*) was influenced by the presence of the predatory pike (*Esox lucius*). The morphology of crucian carp differs between lakes with piscivores and small ponds without predators, with

the lake individuals being more deeper-bodied, which has been attributed to different resource levels. In both field manipulations and laboratory experiments Brönmark and Miner (1992) showed that although the food regime did affect morphology, the influence of a pike sharing the same water and feeding on crucian carps was far more drastic. Brönmark and Pettersson (1994) showed that chemical cues, released when pike or perch feed on carp, induce the change in morphology. The “hunchback” morph benefits from reduced predation because piscivores, such as pike, are gape-limited predators. Thus, by altering the relative body depth crucian carp reaches a predator-safe size refuge at a smaller total body size. Since the “hunchback” phenotype is not always expressed it is most likely associated with a cost, which may be reduced swimming performance (Brönmark and Miner 1992, Brönmark and Pettersson 1994).

Phenotypic plasticity in response to photoperiod is reported from major groups of organisms such as plants, insects, fish, amphibians, reptiles, birds and mammals (Danilevskii 1965, Aschoff 1981, Gwinner 1981, Hoffman 1981, Saunders 1982). Such responses to photoperiod is one of the best examples of plasticity in response to a cue that predicts future conditions, typically the change of season, without having an unspecific and general effect on biochemistry. Among insects, which is the best studied group, photoperiod is known to control or influence traits as diverse as the induction and termination of diapause and migration (Dingle 1978), the induction of seasonal morphs (Shapiro 1976), growth rates (Nylin et al. 1989, Nylin 1992), fecundity, sexual behaviour and sex ratio (Saunders 1982, Tauber et al. 1986). Except for the possibility that the day length could in some cases directly affect the number of hours that can be spent feeding, there are few cases of photoperiodism where we can doubt that it is an adaptation. Often, the problem is more in understanding the exact adaptive nature of the plasticity (if any, in the present environment). Since photoperiodism is such a widespread mechanism in the organic world, testing whether a specific photoperiod reaction norm is an adaptation often requires more than just using the argument that photoperiod is an environmental factor unlikely to produce these phenotypic effects (see discussion in earlier sections). It seems very unlikely that photoperiodic sensitivity has evolved independently in all cases where it has been found.

## Conclusions

Plasticity is a major component of phenotypic variation and has recently attracted much attention as an important factor in evolution. It is clear that plasticity can have a genetic basis, can be adaptive and may be altered by natural selection. Reaction norms of genotypes, widely used to visualise plasticity, have been described as the

basis for the evolution of phenotypic plasticity. We argue that it is often useful to treat modifications of reaction norms as possible adaptations. However, there have been few attempts to generate testable qualitative or quantitative predictions of the presence and shape of reaction norms. Almost universally, adaptive explanations for reaction norms in the literature are ad hoc constructions.

It is often problematic to distinguish between non-adaptive plasticity, caused by physical or chemical constraints, and adaptive plasticity. It is furthermore difficult to show that the plasticity is an adaptation to a certain environment or distribution of environments. In general, the function of a plastic phenotype is less ambiguous for morphological plasticity than for life history plasticity. Often, the link between cause and effect for morphological plasticity is so non-intuitive and “seemingly designed” that the plasticity can be inferred to be a result of natural selection. In such cases comparative studies can be used to identify the distribution and origin of the plasticity in the phylogeny. The above design argument is sometimes also applicable to plasticity in life history traits, but more often the environmental effect is less specific and for this reason both the induction mechanism and the induced phenotypes show few elements of apparent “design”. Frequently, there are alternative explanations for environmentally induced variation in life history traits. Therefore, to determine whether a reaction norm of that kind may be an adaptation to a distribution of environments, additional methods are needed. We argue that a successful research program would include experimental testing of optimality models or reciprocal experiments to establish the adaptiveness of the reaction norm. To furthermore show that the reaction norm is likely to be an adaptation we often need comparative methods, where reaction norm differences between classes of organisms (e.g. sexes, populations, species) are predicted and subsequently investigated. We also argue that it is fruitful to view plasticity of that kind as a result of organisms “choosing” a phenotype on the basis of environmental input, in a manner analogous to how animals take behavioural decisions depending on the situation.

Finally, only in a very few cases have phylogenetic methods been used to demonstrate that a given plasticity is likely to be an adaptation in the historical sense (origin linked to function), and at what point in the phylogeny the evolution of plasticity occurred. More such studies are needed before we can illuminate the key questions regarding the evolution of plasticity: when, why and how does a plastic phenotype evolve in response to heterogeneity of the environment, instead of genetic diversity and, ultimately, speciation? Or, as recently suggested by West-Eberhard (1989), is plasticity the origin of diversity rather than the alternative?

*Acknowledgements* – We thank Stephen Stearns for constructive criticism that greatly improved the manuscript. This study was supported by grants from the Swedish Natural Science Research Council to S.N.

## References

- Adler, F. R. and Harvell, C. D. 1990. Inducible defences, phenotypic variability and biotic environments. – *Trends Ecol. Evol.* 5: 407–410.
- Adler, G. H. and Levins, R. 1994. The island syndrome in rodent populations. – *Q. Rev. Biol.* 69: 473–490.
- Albon, S. D., Mitchell, B. and Staines, B. W. 1983. Fertility and body weight in female red deer: a density-dependent relationship. – *J. Anim. Ecol.* 52: 969–980.
- Andersen, N. M. 1993. The evolution of wing polymorphism in water striders (Gerridae): a phylogenetic approach. – *Oikos* 67: 433–443.
- Aschoff, J. 1981. Annual Rhythms in Man. – In: Aschoff, J. (ed.), *Handbook in behavioral neurobiology*. Plenum Press, New York, pp. 475–487.
- Atkinson, D. 1994. Temperature and organism size – a biological law for ectotherms? – *Adv. Ecol. Res.* 25: 1–58.
- Bernardo, J. 1994. Experimental analysis of allocation in two divergent, natural, salamander populations. – *Am. Nat.* 143: 14–38.
- Berrigan, D. and Charnov, E. L. 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. – *Oikos* 70: 474–478.
- Berven, K. A., Gill, D. E. and Smith-Gill, S. J. 1979. Countergradient selection in the green frog, *Rana clamitans*. – *Evolution* 33: 609–623.
- Blouin, M. S. 1992. Comparing bivariate reaction norms among species: time and size at metamorphosis in three species of *Hyla* (Anura: Hylidae). – *Oecologia* 90: 288–293.
- Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. – *Adv. Genet.* 13: 115–155.
- Bradshaw, W. E. 1976. Geography of photoperiodic response in a diapausing mosquito. – *Nature* 262: 384–385.
- 1990. The present and future of insect life-cycle evolution. – In: Gilbert, F. (ed.), *Insect life cycles*. Springer, London.
- Brakefield, P. M. and Larsen, T. B. 1984. The evolutionary significance of dry and wet season forms in some tropical butterflies. – *Biol. J. Linn. Soc.* 22: 1–12.
- and Reitsma, N. 1991. Phenotypic plasticity, seasonal climate and the population biology of *Bicyclus* butterflies (Satyridae) in Malawi. – *Ecol. Entomol.* 16: 291–303.
- Brönmark, C. and Miner, J. G. 1992. Predator-induced phenotypical change in body morphology in crucian carp. – *Science* 258: 1348–1350.
- and Pettersson, L. 1994. Chemical cues from piscivores induce a change in morphology in crucian carp. – *Oikos* 70: 369–402.
- Brooks, D. R. and McLennan, D. A. 1991. Phylogeny, ecology, and behavior. – Univ. of Chicago Press, Chicago.
- Coddington, J. A. 1988. Cladistic test of adaptational hypotheses. – *Cladistics* 4: 3–22.
- 1994. Homology and convergence in the study of adaptation. – In: Eggleton, P. and Vane-Wright, R. (eds), *Phylogenetics and ecology*. Academic Press, London, pp. 53–78.
- Collins, J. P. and Cheek, J. E. 1983. Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. – *Am. Zool.* 23: 77–84.
- Conover, T. J. and Present, T. M. C. 1990. Countergradient variation in growth rate: compensation for the length of the growing season among Atlantic silversides from different latitudes. – *Oecologia* 83: 316–324.
- Crowl, T. A. and Covich, A. P. 1990. Predator-induced life-history shifts in a freshwater snail. – *Science* 247: 949–951.
- Crump, M. L. 1989. Effect of habitat drying on development time and size at metamorphosis in *Hyla pseudopuma*. – *Copeia* 1989: 794–797.
- Curio, E. 1973. Towards a methodology of telemetry. – *Experientia* 29: 1045–1058.
- Danilevskii, A. S. 1965. Photoperiodism and seasonal development of insects. – Oliver & Boyd, London.
- Darwin, C. 1859. *The origin of species*. (1st ed.). – Murray, London.
- Dingle, H. (ed.). 1978. *Evolution of insect migration and diapause*. – Springer, New York.
- 1992. Food level reaction norms in size-selected milkweed bugs (*Oncopeltus fasciatus*). – *Ecol. Entomol.* 17: 121–126.
- Dodson, S. 1989. Predator-induced reaction norms. – *BioScience* 39: 447–452.
- Felsenstein, J. 1985. Phylogenies and the comparative method. – *Am. Nat.* 125: 1–15.
- Ford, N. B. and Seigel, R. A. 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. – *Ecology* 70: 1768–1774.
- Gilbert, J. J. 1980. Female polymorphism and sexual reproduction in the rotifer *Asplanchna*: evolution of their relationship and control by dietary tocopherol. – *Am. Nat.* 116: 409–431.
- Gould, S. J. and Lewontin, R. C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. – *Proc. Zool. Soc. Lond.* 205: 581–598.
- Gupta, A. P. and Lewontin, R. C. 1982. A study of reaction norms in natural populations of *Drosophila pseudoobscura*. – *Evolution* 36: 934–948.
- Gwinner, E. 1981. Circannual systems. – In: Aschoff, J. (ed.), *Handbook of behavioral neurobiology*. Plenum Press, New York, pp. 391–410.
- Harvell, C. D. and Helling, R. 1993. Experimental induction of localized reproduction in a marine Bryozoan. – *Biol. Bull.* 184: 286–295.
- Harvey, P. H. and Pagel, M. D. 1991. *The comparative method in evolutionary biology*. – Oxford Univ. Press, Oxford.
- Hillesheim, E. and Stearns, S. C. 1991. The responses of *Drosophila melanogaster* to artificial selection on body weight and its phenotypic plasticity in two larval food environments. – *Evolution* 45: 1909–1923.
- Hoffman, K. 1981. Photoperiodism in vertebrates. – In: Aschoff, J. (ed.), *Handbook of behavioral neurobiology*. Plenum Press, New York, pp. 449–473.
- Houston, A. I. and McNamara, J. M. 1992. Phenotypic plasticity as a state-dependent life-history decision. – *Evol. Ecol.* 6: 243–253.
- Huey, R. B. and Kingsolver, J. 1989. Evolution of thermal sensitivity of ectotherm performance. – *Trends Ecol. Evol.* 4: 131–135.
- Jones, S. M. and Ballinger, R. E. 1987. Comparative life histories of *Holbrookia maculata* and *Sceloporus undulatus* in western Nebraska. – *Ecology* 68: 1828–1838.
- Jorgenson, J. T., Festa-Bianchet, M., Lucherini, M. and Wiselhart, W. D. 1993. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. – *Can. J. Zool.* 71: 2509–2517.
- Kaitala, A. 1987. Dynamic life-history strategy of the waterstrider *Gerris thoracicus* as an adaptation to food and habitat variation. – *Oikos* 48: 125–131.
- 1991. Phenotypic plasticity in reproductive behaviour of waterstriders: trade-offs between reproduction and longevity during food stress. – *Funct. Ecol.* 5: 12–18.
- Kawecki, T. J. and Stearns, S. C. 1993. The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. – *Evol. Ecol.* 7: 155–174.
- Leimar, O., Karlsson, B. and Wiklund, C. 1994. Unpredictable food and sexual size dimorphism in insects. – *Proc. R. Soc. Lond. B.* 258: 121–125.
- Lewontin, R. C. 1978. Adaptation. – *Sci. Am.* 239: 212–230.
- Lüning, J. 1994. Anti-predator defenses in *Daphnia* – are life-history changes always linked to induced neck spines? – *Oikos* 69: 427–436.
- Madsen, T. and Shine, R. 1993. Phenotypic plasticity in body size and sexual size dimorphism in European grass snakes. – *Evolution* 47: 321–325.
- Masaki, S. 1978. Seasonal and latitudinal adaptations in the life cycles of crickets. – In: Dingle, H. (ed.), *Evolution of insect migration and diapause*. Springer, New York, pp. 000–000.

- Meffe, G. K. 1992. Plasticity of life-history characters in eastern mosquitofish (*Gambusia holbrooki*: Poeciliidae) in response to thermal stress. – *Copeia* 1992: 94–102.
- Merrifield, F. and Poulton, E. B. 1899. The colour relation between the pupae of *Papilio machaon*, *Pieris napi* and many other species, and the surroundings of the larvae preparing to pupate. – *Trans. Entomol. Soc. Lond.* 1899: 369–433.
- Negus, N. C. and Berger, P. J. 1992. Phenotypic plasticity of the montane vole (*Microtus montanus*) in unpredictable environments. – *Can. J. Zool.* 70: 2121–2124.
- Newman, R. A. 1988a. Adaptive plasticity in development of *Scaphiopus couchi couchi* tadpoles in desert ponds. – *Evolution* 42: 774–783.
- 1988b. Genetic variation for larval anuran (*Scaphiopus couchi*) development time in an uncertain environment. – *Evolution* 42: 763–773.
- 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. – *Ecology* 70: 1775–1787.
- 1992. Adaptive plasticity in amphibian metamorphosis. – *BioScience* 42: 671–678.
- Niewiarowski, P. H. and Roosenburg, W. 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. – *Ecology* 74: 1992–2002.
- Nylin, S. 1991. Butterfly life history adaptations in seasonal environments. – Ph.D. thesis, Univ. of Stockholm.
- 1992. Seasonal plasticity in life history traits: growth and development in *Polygonia c-album* (Lepidoptera: Nymphalidae). – *Biol. J. Linn. Soc.* 47: 301–323.
- 1994. Seasonal plasticity and life-cycle adaptations in butterflies. – In: Danks, H. V. (ed.), *Insect life cycle polymorphism*. Kluwer, Dordrecht, pp. 41–67.
- and Svård, L. 1990. Latitudinal patterns in the size of European butterflies. – *Holarct. Ecol.* 14: 192–202.
- , Wickman, P.-O. and Wiklund, C. 1989. Seasonal plasticity in growth and development of the speckled wood butterfly, *Pararge aegeria* (Satyriinae). – *Biol. J. Linn. Soc.* 38: 155–171.
- , Wickman, P.-O. and Wiklund, C. In press. Life cycle regulation and life history plasticity in the speckled wood butterfly: are reaction norms predictable? – *Biol. J. Linn. Soc.*
- Pagel, M. 1994. The adaptationist wager. – In: Eggleton, P. and Vane-Wright, R. (eds), *Phylogenetics and ecology*. Academic Press, London, pp. 29–51.
- Parejeko, K. and Dodson, S. I. 1991. The evolutionary ecology of an antipredator reaction norm: *Daphnia pulex* and *Chaoborus americanus*. – *Evolution* 45: 1665–1674.
- Petranka, J. W. and Sih, A. 1987. Habitat duration, length of larval period, and the evolution of a complex life cycle of a salamander, *Ambystoma texanum*. – *Evolution* 41: 1347–1356.
- Radwan, J. 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlessei*. – *Behav. Ecol. Sociobiol.* 33: 201–208.
- Reznick, D. and Yang, A. P. 1993. The influence of fluctuating resources on life history – patterns of allocation and plasticity in female guppies. – *Ecology* 74: 2011–2019.
- Riessen, H. P. and Sprules, G. W. 1990. Demographic costs of an antipredator defense in *Daphnia pulex*. – *Ecology* 71: 1536–1546.
- Roff, D. A. 1980. Optimizing development time in a seasonal environment: the ‘ups and downs’ of clinal variation. – *Oecologia* 45: 202–208.
- 1983. Phenological adaptation in a seasonal environment: A theoretical perspective. – In: Brown, V. K. and Hodek, I. (eds), *Diapause and life cycle strategies in insects*. Junk, The Hague, pp. 253–270.
- Sæther, B.-E. and Heim, M. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. – *J. Anim. Ecol.* 62: 482–489.
- Saunders, D. S. 1982. *Insect clocks*. – Pergamon Press, Oxford.
- Scharloo, W. 1989. Developmental and physiological aspects of reaction norms. – *BioScience* 39: 465–471.
- Scheiner, S. M. 1993a. Genetics and evolution of phenotypic plasticity. – *Annu. Rev. Ecol. Syst.* 24: 35–68.
- 1993b. Plasticity as a selectable trait: reply to Via. – *Am. Nat.* 142: 371–373.
- and Lyman, R. F. 1989. The genetics of phenotypic plasticity. I Heritability. – *J. Evol. Biol.* 2: 95–107.
- Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. – *Annu. Rev. Ecol. Syst.* 17: 667–693.
- 1989. Phenotypic integration and environmental change. – *BioScience* 39: 460–464.
- and Pigliucci, M. 1993. Control of phenotypic plasticity via regulatory genes. – *Am. Nat.* 142: 366–370.
- Schmalhausen, I. I. 1949. *Factors of evolution*. – Univ. of Chicago Press, Chicago.
- Semlitsch, R. D. 1993. Asymmetric competition in mixed populations of tadpoles of the hybridogenetic *Rana esculenta* complex. – *Evolution* 47: 510–519.
- and Gibbons, J. W. 1985. Phenotypic variation in metamorphosis and paedomorphosis in the salamander *Ambystoma talpoideum*. – *Ecology* 66: 1123–1130.
- and Wilbur, H. M. 1988. Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. – *Copeia* 1988: 978–983.
- , Harris, R. N. and Wilbur, H. M. 1990. Paedomorphosis in *Ambystoma talpoideum*: maintenance of population variation and alternative life-history pathways. – *Evolution* 44: 1604–1613.
- Shapiro, A. M. 1976. Seasonal polyphenism. – *Evol. Biol.* 9: 259–333.
- 1984. The genetics of seasonal polyphenism and the evolution of “general purpose genotypes” in butterflies. – In: Wöhrmann, K. and Loeschcke, V. (eds), *Population biology and evolution*. Springer, Berlin, pp. 16–30.
- Sibly, R. M. and Atkinson, D. 1994. How rearing temperature affects optimal adult size in ectotherms. – *Funct. Ecol.* 8: 486–493.
- Stearns, S. C. 1986. Natural selection and fitness, adaptation and constraint. – In: Raup, D. M. and Jablonski, D. (eds), *Patterns and processes in the history of life*. Springer, Heidelberg, pp. 23–44.
- 1989. The evolutionary significance of phenotypic plasticity. – *BioScience* 39: 436–445.
- 1992. The evolution of life histories. – Oxford Univ. Press, Oxford.
- and Koella, J. C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. – *Evolution* 40: 893–913.
- , de Jong, G. and Newman, R. 1991. The effects of phenotypic plasticity on genetic correlations. – *Trends Ecol. Evol.* 6: 122–126.
- Stemberger, S. S. and Gilbert, J. J. 1987. Multiple-species induction of morphological defenses in the rotifer *Keratella testudo*. – *Ecology* 68: 370–378.
- Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. – *Evol. Biol.* 21: 127–178.
- Tauber, M. J., Tauber, C. A. and Masaki, S. 1986. *Seasonal adaptations of insects*. – Oxford Univ. Press, Oxford.
- Tejedo, M. and Reques, R. 1994. Plasticity in metamorphic traits of natterjack tadpoles: the interactive effects of density and pond duration. – *Oikos* 71: 295–304.
- Timms, S., Ferro, D. N. and Waller, J. B. 1981. Andropoly-morphism and its heritability in *Sancassania berlessei* (Michael) (Acari: Acaridae). – *Acarologia* 22: 391–398.
- van Noordwijk, A. J. 1989. Reaction norms in genetical ecology. – *BioScience* 39: 453–458.
- Väpsäläinen, K. 1978. Wing dimorphism and diapause in *Geris*: Determination and adaptive significance. – In: Dingle,

- H. (ed.), Evolution of insect migration and diapause. Springer, New York, 218–253.
- Via, S. 1987. Genetic constraints on the evolution of phenotypic plasticity. – In: Loeschcke, V. (ed.), Genetic constraints on adaptive evolution. Springer, New York, pp. 47–71.
- 1993a. Adaptive phenotypic plasticity: target or by-product of selection in a variable environment? – *Am. Nat.* 142: 352–365.
- 1993b. Regulatory genes and reaction norms. – *Am. Nat.* 142: 374–378.
- and Lande, R. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. – *Evolution* 39: 505–522.
- and Lande, R. 1987. Evolution of genetic variability in a spatially heterogeneous environment: effects of genotype-environment interaction. – *Gen. Res.* 49: 147–156.
- Walls, S. S., Beatty, J. J., Tissot, B. N., Hokit, D. G. and Blaustein, A. R. 1993a. Morphological variation and cannibalism in a larval salamander (*Ambystoma macrodactylum columbianum*). – *Can. J. Zool.* 71: 1543–1551.
- , Belanger, S. S. and Blaustein, A. R. 1993b. Morphological variation in a larval salamander – dietary induction of plasticity in head shape. – *Oecologia* 96: 162–168.
- Wanntorp, H.-E. 1983. Historical constraints in adaptation theory: traits and non-traits. – *Oikos* 41: 157–159.
- Watt, W. B. 1968. Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. – *Evolution* 2: 437–458.
- 1969. Adaptive significance of pigment polymorphisms in *Colias* butterflies. II. Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*. – *Proc. Natl. Acad. Sci. USA* 63: 767–774.
- West-Eberhart, M. J. 1989. Phenotypic plasticity and the origins of diversity. – *Annu. Rev. Ecol. Syst.* 20: 249–278.
- Wiklund, C. 1975. Pupal colour polymorphism in *Papilio machaon* L. and the survival in the field of cryptic versus non-cryptic pupae. – *Trans. R. Entomol. Soc. Lond.* 127: 73–84.
- , Nylin, S. and Forsberg, J. 1991. Sex-related variation in growth rate as a result of selection for large size and protandry in a bivoltine butterfly, *Pieris napi*. – *Oikos* 60: 241–250.
- Williams, G. C. 1966. Adaptation and natural selection. – Princeton Univ. Press, Princeton, NJ.
- 1992. Natural selection. Domains, levels, and challenges. – Oxford Univ. Press, Oxford.
- Windig, J. J. 1993. The genetic background of plasticity in wing patterns of *Bicyclus* butterflies. – Ph.D. thesis, Univ. of Leiden.
- 1994. Genetic correlations and reaction norms in wing pattern of the tropical butterfly *Bicyclus anynana*. – *Heredity* 73: 459–470.
- Woltereck, R. 1909. Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterscheide bei Daphniden. – *Ver. Deutsch. Zool. Ges.* 1909: 110–172.