



Phenotypic flexibility and the evolution of organismal design

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Evolutionary biologists often use phenotypic differences between species and between individuals to gain an understanding of organismal design. The focus of much recent attention has been on developmental plasticity – the environmentally induced variability during development within a single genotype. The phenotypic variation expressed by single reproductively mature organisms throughout their life, traditionally the subject of many physiological studies, has remained underexploited in evolutionary biology. Phenotypic flexibility, the reversible within-individual variation, is a function of environmental conditions varying predictably (e.g. with season), or of more stochastic fluctuations in the environment. Here, we provide a common framework to bring the different categories of phenotypic plasticity together, and emphasize perspectives on adaptation that reversible types of plasticity might provide. We argue that better recognition and use of the various levels of phenotypic variation will increase the scope for phenotypic experimentation, comparison and integration.

There is an increasing trend in exploiting phenotypic variability within single genotypes (phenotypic plasticity) to answer questions about organismal design and adaptation [1–11]. However, all of these studies focus strongly on only one level of phenotypic plasticity – that described by the term ‘developmental plasticity’. This is the irreversible variation in the traits of individuals that results from processes during development as a consequence of variation in the environment and is described by empirical relationships known as reaction norms [8,12]. The related concept of ‘polyphenism’ refers to the ability of some arthropods and other invertebrate organisms to produce a sequence of generations with different discrete phenotypes in the course of a season to accommodate seasonal changes in the environment [13,14].

At the same time, there is an opposite trend, the tendency to apply the term ‘phenotypic plasticity’ to all context-dependent variation in behaviour [15,16], or to the many reversible metabolic or endocrine switches within single organisms that are initiated by changes in the external environment. This is the subject of most physiological research [17]. The confusion arising from such unconditional use of the term phenotypic plasticity

stems from the range of phenomena that are referred to by that one term. A similar problem haunts discussions of experimental studies of ‘acclimation’ and ‘acclimatization’, the adjustments of physiological traits to ambient environmental conditions in the laboratory and the field, respectively [18,19,20]. We believe that all these cases should be referred to as phenotypic flexibility, which has the advantage of being played out within single individuals (and genotypes).

We propose that defining characters of four categories of phenotypic plasticity are whether phenotypic changes are reversible within a single individual organism, and whether the changes are cyclic (Table 1). Considering these distinct types of phenotypic plasticity, we examine the ways in which they can help us to understand organismal design. Given the paucity of previous attention (see [21,22]), we focus on the intra-individual and reversible phenotypic transformations for which the shorthand ‘phenotypic flexibility’ was recently coined [23,24].

Phenotypic flexibility

When environmental conditions change rapidly and over shorter timescales than a lifetime, individuals that can show continuous but reversible transformations in behaviour, physiology and morphology might incur a selective advantage [18,22,25]. There are now several studies documenting substantial but reversible phenotypic changes within adult organisms, especially with regard to the sizes of organ systems in relation to metabolic demand [23,26,27].

The most dramatic examples of reversible phenotypic change are those organisms in which the reproductively

Table 1. Mutually exclusive definitions of the four most commonly historically used categories of phenotypic plasticity^{a,b}

Plasticity category	Phenotypic change is reversible	Variability occurs within a single individual	Phenotypic change is seasonally cyclic ^b
Developmental plasticity	No	No	No
Polyphenism ^c	No	No	Yes
Phenotypic flexibility	Yes	Yes	No
Life-cycle staging ^c	Yes	Yes	Yes

^aPhenotypic plasticity itself indicates the general capacity for change or transformation within genotypes in response to different environmental conditions.

^bPrevious workers might have used less restrictive definitions.

^cCan be regarded as a subcategory of developmental plasticity; life-cycle staging is a subcategory of phenotypic flexibility.

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active phenotypes shrink in overall body size. Caribbean sea urchins *Diadema antillarum* have a hard calcite skeleton but are able to shift body size in response to variations in local food conditions [28]. Levitan experimentally altered competitor densities, and showed that body size increased and decreased to levels predicted from field-based food abundance–body size relationships (Fig. 1). By adjusting structural body size, the urchins reduced maintenance costs and thereby optimized reproduction and survival according to local food availability [28]. Although body size altered, the mouth structures (Aristotle's lantern) of the urchins, and thus their capacity to eat, remained unchanged [29].

When crustaceans moult their external skeleton, they normally increase in size. Nevertheless, similar to the sea urchins, krill *Euphausia pacifica* can adjust to extended periods of abnormally high energy expenditure (owing to

increased water temperatures) by moulting to reduce their body size [30]. A particularly striking demonstration that food availability influences optimal body size, and that fitness increases with a reduced body size when food is limited, has also been provided for a vertebrate, the marine iguana *Amblyrhynchus cristatus* from the Galápagos archipelago (Box 1). However, in snakes, a group of reptiles famous for the flexibility of their digestive organs [31,32], whole-body shrinkage under food limitation could not be demonstrated [33].

Changes in the size of body parts rather than of the body as a whole occur in a wide variety of marine invertebrates. For example, the demosponge *Halichondria panicea* responds to changes in wave energy [34] by increasing its skeletal stiffness as the wave energy

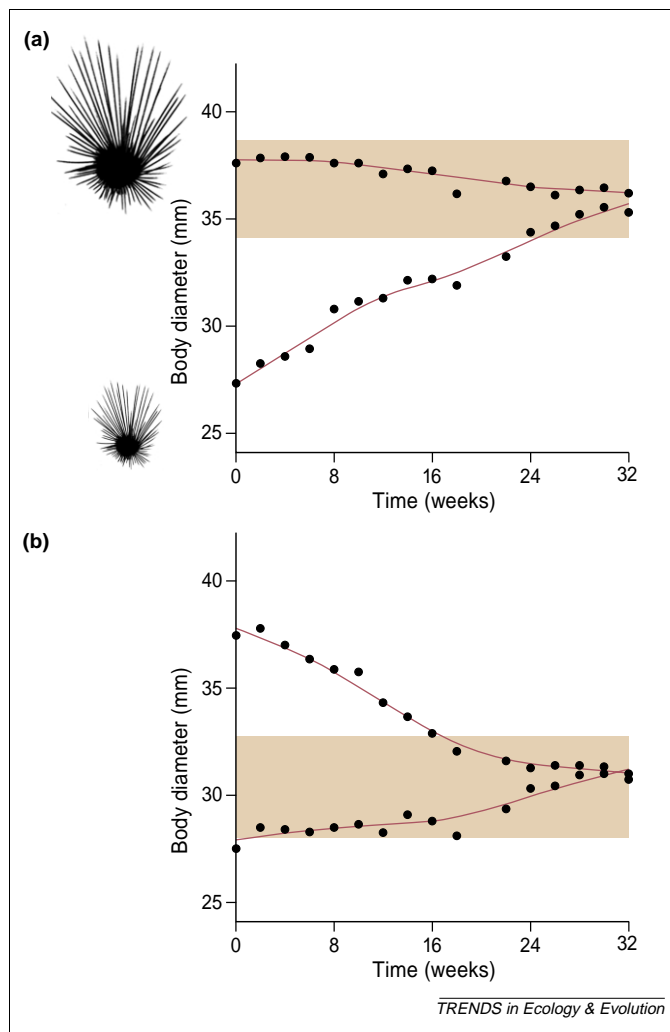


Fig. 1. Body-size adjustment as a function of competitor density and/or food availability. Sea urchins *Diadema antillarum* from the Virgin Islands in the Caribbean adjust body size in proportion to the density of their population, which is correlated with food availability. When the population density is low (i.e. relatively high food availability) (a) the large and small sea urchins converge to the same large body size over the course of eight months (as predicted, indicated by the shaded bar). Under a high urchin density regime (i.e. relatively low food abundance) (b), large and small individuals converge to the much smaller size, as predicted (shaded bar). Based on data from [28] for 144 individuals kept in 32 cage enclosures with stocking densities of three or six animals per cage. Body size predictions are generated from field correlations with food availability.

Box 1. Adaptive value of the shrinking bodies of marine iguanas

Marine iguanas *Amblyrhynchus cristatus* inhabit the rocky shores of the Galápagos islands, where they graze algae in the intertidal and the nearshore subtidal areas. In coastal areas with a high food abundance (indicated by the length and turnover of algal swards [69]), marine iguanas tend to be larger than in areas where food is scarce. However, small individuals outcompete large individuals when food is limited because small individuals are more efficient grazers [69].

Food availability is strongly influenced by the El Niño Southern Oscillation (ENSO). During ENSO events, warm nutrient-poor water reduces the growth of algae, causing food availability for marine iguanas to be limited for months or even years. The largest animals (the males) are the first to die during such events [70]. However, individuals respond by adjusting their individual phenotype. During periods of food limitation, the body length of individual marine iguanas decreases by as much as 20% [71]. The magnitude of the decrease is positively correlated with the likelihood of survival (Fig. 1). The higher survival rates might be a consequence of a reduction of maintenance costs when the structural parts of the body shrink, and smaller animals can survive for longer than larger animals at lower standing stocks of algae. Thus, in marine iguanas, shrinkage does not result in death, but rather appears to be a strategic response to food scarcity.

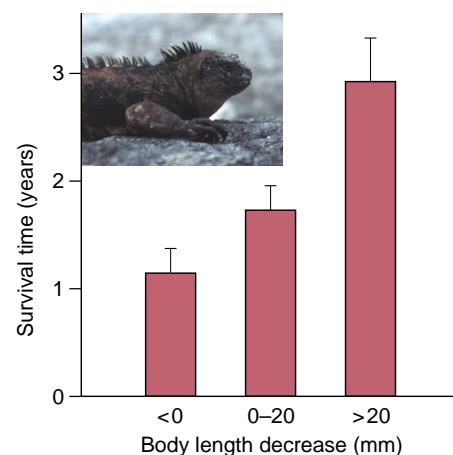


Fig. 1. Survival time for marine iguanas after various degrees of body shrinkage in response to food limitation. On the island of Santa Fé, adult individual marine iguanas that shrank the most during the 1992–1993 ENSO event (measured in January–March 1992 and again a year later), survived longer after March 1993 compared with individuals that did not shrink so much. Based on data from [71].

increases, and vice versa. In bivalves, the feeding apparatus comprises the gills, which generate a water flow from which they retrieve particulate matter, and the labial palps, which sort food items from the trapped material. Using reciprocal transplant experiments with blue mussels *Mytilus edulis*, Essink *et al.* demonstrated that the higher the load of suspended matter (more particles but with a lower quality), the smaller the gills and the larger the palps [35]. Pacific oysters *Crassostrea gigas* also show adjustments to the sizes of palps and gills with season (Fig. 2). Again, the reversible changes appear to be driven by changes in food availability: the growth of the pumps relative to the sorting machinery resulted in more efficient foraging when food was abundant [36].

When food availability is low in winter, sea cucumbers *Parastichopus californicus* temporarily reduce the size of their alimentary canal [37,38]. Changes in gut size have also been described for several bird species [39,40]. For example, a change in diet resulted in marked reversible changes in gizzard size for both Japanese quail *Coturnix japonica* [41] and red knots *Calidris canutus* [42] (Fig. 3). The approximate halvings and doublings of gizzard mass occurred within 1–2 weeks of the change in diet. These changes in organ size illustrate how phenotypic flexibility can help us to unravel the way in which organisms solve problems of allocation resulting from competing ecological demands [43].

Cyclic phenotypic variation: the life-cycle stage concept

In seasonal environments, different activities related to reproduction and survival (breeding, moult, migration, hibernation, etc.) are usually separated in time within individuals, and tend to occur at predictable times of the year, accompanied by changes in the mature adult phenotype [44]. To perform optimally under a wide range of environmental conditions (variations that are often cyclic) by tracking or anticipating the external changes, a long-lived individual must regulate gene expression to adjust its

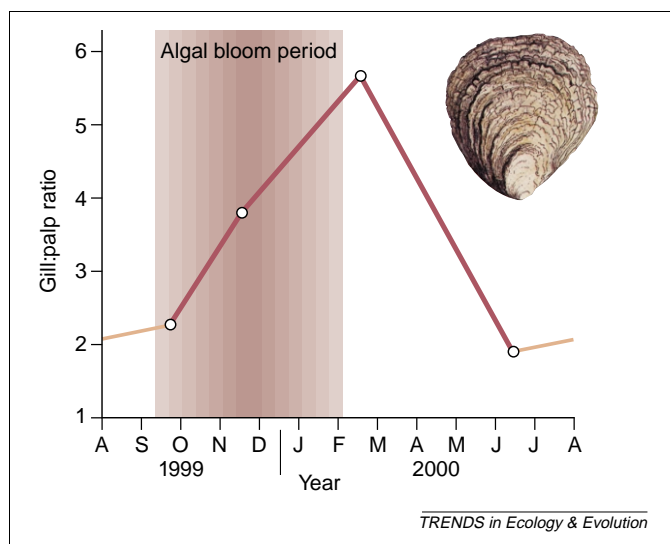


Fig. 2. Seasonal cycle of the gill:palp ratio in Pacific oysters *Crassostrea gigas* in eastern Australia in relation to the occurrence of blooms of their phytoplankton food (shaded area). Based on data from [36].

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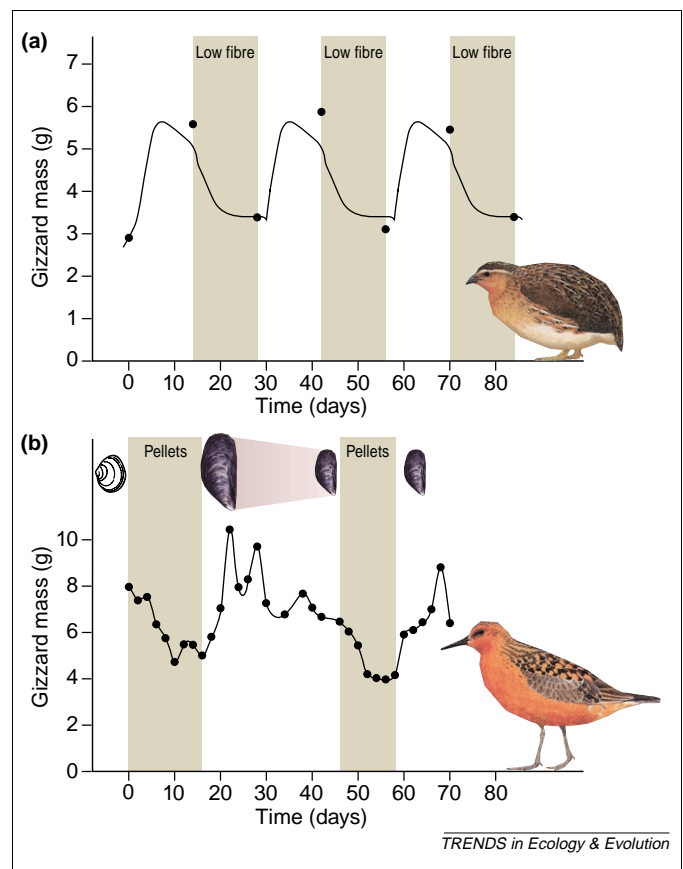


Fig. 3. Reversible size changes in the gizzards of adult Japanese quail *Coturnix japonica* (a) and red knots *Calidris canutus* (b). The quail were given a diet of alternately low or high nondigestible fibre content (3% and 45%, respectively). Within 14 days, they showed a doubling of the size of the gizzard. Red knots are specialized molluscivore shorebirds with strong muscular gizzards, which they use to crush ingested hard-shelled prey. With a change in diet from medium–small mussels *Mytilus edulis* ingested whole (the smallest size classes are easiest to crush) to a diet of soft food-pellets, gizzard mass halved within the first eight days following the diet shift. Shifts from a pellet to a mussel diet induced doublings of gizzard mass within even shorter periods of time. The data for quail were based on the dissection of samples on the day of the diet switch, whereas, in red knots, gizzard size of individuals was monitored with the use of ultrasonography. In quail, the precise time course of size changes was also studied with the use of ultrasonography, but only in one group. The pattern found in the latter group is repeated in (a) to illustrate the probable time course of the changes. Based on data from [41] and [42], respectively.

morphology, physiology and behaviour [18]. The cyclically varying phenotypic expressions of these adjustments within an individual organism are termed 'life-cycle stages' [45,46].

A good example is the plumage changes of the rock ptarmigan *Lagopus mutus*, a species of grouse that lives on the Arctic tundra. For most of the year, the tundra is covered by snow, and both sexes are camouflaged by white plumage [47]. In the brief Arctic spring, when the snow melts and is replaced by summer tundra, the females moult their white plumage in favour of green and brown feathers (Fig. 1). However, the males do not moult their white feathers, and instead appear exceptionally conspicuous, becoming not only attractive to prospecting females, but also easy targets for hunting gyrfalcons *Falco rusticolus*. When opportunities for matings disappear, they attempt to camouflage themselves by soiling their white plumage and are dirtiest at the start of incubation [47]. Only when a clutch is lost to predators and their

mates become fertile again, do the males clean up. They eventually moult into a cryptic summer plumage once the mating season has ended.

The nature of plasticity in environments differing in predictability

The accuracy with which future environmental conditions can be predicted could determine the kind of phenotypic plasticity that one might expect to evolve [25,48,49]. In unpredictable environments, a capacity for rapid and reversible phenotypic change (flexibility) will have obvious fitness payoffs [25]. Where environmental conditions vary in a temporarily predictable way, long-lived organisms can anticipate the changes by showing sequences of life-cycle stages [39,45]. The seasonal template for such sequences might be provided by the natural photoperiodic rhythm and/or by an endogenous circannual pacemaker [50]. In addition, temperature, rainfall, food or densities of conspecifics might give supplementary information, which individuals could use to 'fine-tune' the timing of their phenotypic transformations [51]. The polyphenisms of short-lived organisms, such as some insects, reflect a similar strategy [13].

If there is insufficient environmental information, or if the wrong environmental information is used, an organism might end up with a phenotype that does not quite match its current environment [52]. Indeed, such mismatches are considered to be one of the main costs of developmental plasticity [53]. However, this potential cost disappears for organisms that are capable of fast and reversible phenotypic change. Our traditional focus on the irreversible kinds of plasticity has consequently hindered the development of evolutionary models of phenotypic plasticity ever since the first attempt by Via and Lande [54]. Although quantitative genetic models of developmental plasticity using reaction norms have become quite advanced [6,55], there has been no elaboration of the different levels of plasticity described here. Including a

broader perspective of plasticity in theoretical models (Box 2) will increase the scope for determining the evolutionary stability of phenotypic plasticity.

Interpreting phenotypic flexibility: a study of adaptation?

In evolutionary biology, a phenotypic trait can be considered to be an adaptation only if there is evidence that it has been moulded in specific ways during its evolutionary history to make it more effective for its particular role [56]. Together with Feder and Watt [57,58], we believe that the functional study of phenotype–environment interactions is necessary for evolutionary insight; that is, an 'amechanistic' worldview is no longer satisfactory [58]. Rather than emphasizing that a capacity for phenotypic change is an adaptation (which it might well be [11]), we argue that intra-individual trait variation itself should be used to evaluate the 'goodness of design' criterion for phenotypic adaptation [59].

One of the ways in which phenotypic flexibility is useful is in providing phenotypic variants that are also characteristic of related species that do not show such variability. For example, the study of rock ptarmigan (Fig. 4) illustrated how comparisons among intra-individual variants of the phenotype can yield strong inferences about function. In this case, the visual aspect of the plumage in females was determined by its role for camouflage only. In males, the plumage not only served the dual role of camouflage in winter (when white) and in late summer (when comprising a cryptic patterning of browns), but also the sexually selected, ornamental role (white) in the mating season. The soiling of the white plumage when mating opportunities were no longer present (but when the moult into a cryptic plumage has not yet begun) provides a behavioural 'quick fix' to a crucial allocation problem. The close match between the changing aspects of the tundra and that of rock ptarmigan plumage supports the notion that the large variety of winter plumage in

Box 2. A quantitative genetic framework that includes phenotypic flexibility

The total phenotypic variance (σ_T^2) of a population can be divided into different components. Traditionally, these include a genotypic (G) and an environmental component (E), as well as a genotype \times environment interaction (G \times E) and an error term e . This can be written formally as Eqn I:

$$\sigma_T^2 = \sigma_G^2 + \sigma_E^2 + \sigma_{G \times E}^2 + e \quad [\text{Eqn I}]$$

Often, the genotypic component G is divided into (1) additive; (2) dominance; and (3) epistatic effects. However, phenotypic measures can vary over time within an individual [21]. Often, the main interest of quantitative genetic studies is an estimation of the heritable fraction of phenotypic variation. Additional variance components, such as within-individual variation, are considered to be noise that reduces the accuracy of the estimates. Although Lynch and Walsh [72] acknowledge the presence of nonlabile and labile traits, these additional variance components are considered jointly and do not receive separate analysis.

However, analogous to the partitioning of genotypic components, the environmental component can be divided into separate factors. We propose these to be a reversible σ_{EF}^2 (using the F of flexibility) and an irreversible fraction σ_{EP}^2 (using the P of plasticity) of phenotypic

variance. Together with the relevant interaction terms, this yields Eqn II:

$$\sigma_T^2 = \sigma_G^2 + \sigma_{EP}^2 + \sigma_{EF}^2 + \sigma_{G \times EP}^2 + \sigma_{G \times EF}^2 + \sigma_{EP \times EF}^2 + \sigma_{G \times EP \times EF}^2 + e \quad [\text{Eqn II}]$$

When dealing with phenotypic flexibility, we are concerned with a single genotype only. This means that $\sigma_G^2 = 0$, thus reducing Eqn II to Eqn III:

$$\sigma_T^2 = \sigma_{EP}^2 + \sigma_{EF}^2 + \sigma_{EP \times EF}^2 + e \quad [\text{Eqn III}]$$

A clear separation of the reversible and nonreversible components of plasticity enables us to quantify not only the importance of the two separate factors in shaping the phenotype, but also the interaction between them. The interaction term indicates the extent to which reversible variations depend on developmental stage, that is, on the irreversible component. In a review of phenotypic plasticity in African cichlids, Witte *et al.* [73] concluded that phenotypic responses are a function of ontogenetic stage. The further development has progressed, the smaller the flexibility to modify the phenotype becomes (see also [74]). This within-individual variation can readily be captured by the three proposed variance components, that is, a genetic component and two environmental components (a reversible and an irreversible one).

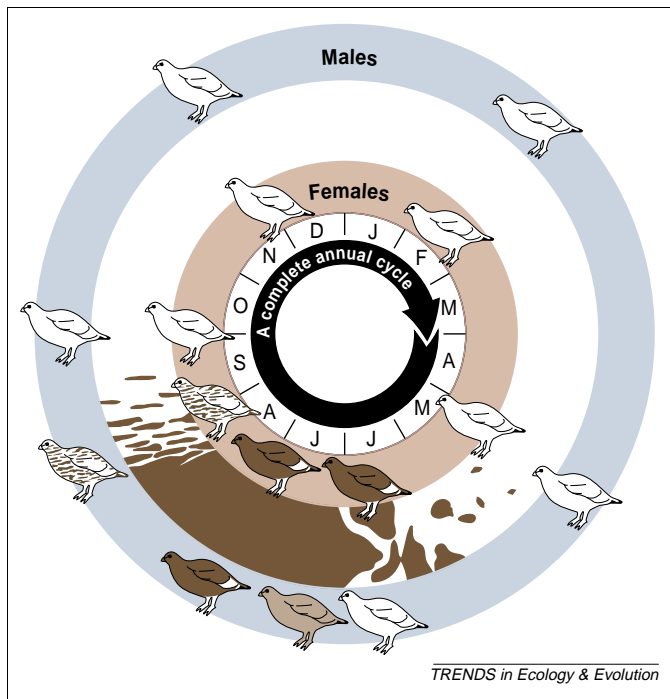


Fig. 4. Annual cycle of the external appearance of male and female rock ptarmigan *Lagopus mutus* in the Canadian Arctic in relation to changes in the camouflage afforded by the tundra habitat (indicated by the appearance of the second circle). This illustrates the power with which such intra-individual changes can be interpreted in a functional context. The changes in plumage represent a change in feathers, except for the change from a pure white to a dirty white colour of males in late June–July, which is the result of soiling. Based partly on data from [47].

different species and subspecies of ptarmigan [60] is likely to reflect adaptations for camouflage.

Thus, intra-individual phenotypic variations can demonstrate how alternative phenotypes represent a single adaptation (camouflage) or different adaptations (camouflage versus sexually selected conspicuousness). This might be particularly appropriate when interspecific comparisons cannot be made. For example, to overcome the absence of matched food-specialists within the same taxon when studying digestive adaptations, Levey and Karasov [61] compared the flexible phenotypes of bird species that were primarily frugivorous in autumn and insectivorous in spring.

Perhaps most importantly, the presence of reversible intra-individual phenotypic variation gives us a powerful tool to use in experimental studies of phenotypic design, almost in the same way that behavioural ecologists have so successfully experimentally unravelled the functions of behavioural traits [62]. For example, the idea that the large muscular gizzards of birds eating hard-shelled prey are an adaptation [63] would be supported by the finding that red knots showing an increased gizzard size with a shift from soft to hard food also have an increased capacity to process the hard food [39], and vice versa. Even better evidence for the adaptive value of gizzard flexibility would be the finding that mussel-fed individuals with the fastest increase in gizzard size (and intake rates) also have the highest fitness. In cases where enough is known about the control mechanisms of the flexible phenotype, there are opportunities for phenotypic engineering, such as the use of hormonal treatments [64,65], to study phenotypic adaptation.

Conclusions

Our discussion complements three recent books about phenotypic plasticity [3,8,11] and two reviews of evolutionary and ecological physiology [66,67]. It enlarges the scope of their viewpoints to bring the various kinds of phenotypic variation together within a common framework and it emphasizes the potential of intra-individual phenotypic variation for biological discovery (see [68] for a discussion that includes variation between genotypes). The extent to which individuals can respond to variations in ecological roles and environment by reversible phenotypic transformations (phenotypic flexibility) is as much part of the life history of organisms as is the variation in fixed traits between individuals that arise as a consequence of differences in developmental conditions (developmental plasticity) [46]. Although the very nature of reversible intra-individual variations makes them harder to describe and incorporate into our thinking about organismal design than is inter-individual variation in fixed traits, they do have the clear advantage of being generated by a single genotype (Box 2). Intra-individual variation readily provides insights into the links between phenotypic design, ecological demand functions (performance) and fitness [57].

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References

- West-Eberhart, M.J. (1989) Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* 20, 249–278
- Gordon, D.M. (1992) Phenotypic plasticity. In *Keywords in Evolutionary Biology* (Keller, E.F. and Lloyd, E.A., eds) pp. 255–262, Harvard University Press
- Rollo, C.D. (1994) *Phenotypes: Their Epigenetics, Ecology and Evolution*, Chapman & Hall
- Travis, J. (1994) Evaluating the adaptive role of morphological plasticity. In *Ecological Morphology: Integrative Organismal Biology* (Wainwright, P.C. and Reilly, S.M., eds) pp. 99–122, Chicago University Press
- Sultan, S.E. (1995) Phenotypic plasticity and plant adaptation. *Acta Bot. Neerl.* 44, 363–383
- Via, S. *et al.* (1995) Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.* 10, 212–217
- Reznick, D. and Travis, J. (1996) The empirical study of adaptation in natural populations. In *Adaptation* (Rose, M.R. and Lauder, G.V., eds) pp. 243–289, Academic Press
- Schlichting, C.D. and Pigliucci, M. (1998) *Phenotypic Evolution: A Reaction Norm Perspective*, Sinauer
- Travis, J. *et al.* (1999) Sources of variation in physiological phenotypes and their evolutionary significance. *Am. Zool.* 39, 422–433
- Chapman, L.J. *et al.* (2000) Phenotypic plasticity and the possible role of genetic assimilation: hypoxia-induced trade-offs in the morphological traits of an African cichlid. *Ecol. Lett.* 3, 387–393
- Pigliucci, M. (2001) *Phenotypic Plasticity*, John Hopkins University Press
- Stearns, S. (1989) The evolutionary significance of phenotypic plasticity. *Bioscience* 39, 436–445
- Shapiro, A.M. (1976) Seasonal polyphenism. *Evol. Biol.* 9, 259–333
- Danks, H.V. (1999) Life cycles in polar arthropods – flexible or programmed? *Eur. J. Entomol.* 96, 83–103

- 15 Komers, P.E. (1997) Behavioural plasticity in variable environments. *Can. J. Zool.* 75, 161–169
- 16 Ghalambor, C.K. and Martin, T.E. (2002) Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behav. Ecol.* 13, 101–108
- 17 Prosser, C.L. (1991) *Environmental and Metabolic Animal Physiology: Comparative Animal Physiology*, 4th edn, Wiley-Liss
- 18 Willmer, P. *et al.* (2000) *Environmental Physiology of Animals*, Blackwell Science
- 19 Wilson, R.S. and Franklin, C.E. (2002) Testing the beneficial acclimation hypothesis. *Trends Ecol. Evol.* 17, 66–70
- 20 Woods, A.H. and Harrison, J.F. (2002) Interpreting rejections of the beneficial acclimation hypothesis: when is physiological plasticity adaptive? *Evolution* 56, 1863–1866
- 21 Scheiner, S.M. (1993) Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* 24, 35–68
- 22 Kingsolver, J.G. and Huey, R.B. (1998) Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. *Am. Zool.* 38, 545–560
- 23 Piersma, T. and Lindström, Å. (1997) Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends Ecol. Evol.* 12, 134–138
- 24 Starck, J.M. (1999) Structural flexibility of the gastro-intestinal tract of vertebrates – implications for evolutionary morphology. *Zool. Anz.* 238, 87–101
- 25 Padilla, D.K. and Adolph, S.C. (1996) Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evol. Ecol.* 10, 105–107
- 26 Hammond, K.A. *et al.* (2001) Effects of altitude and temperature on organ phenotypic plasticity along an altitudinal gradient. *J. Exp. Biol.* 204, 1991–2000
- 27 Starck, J.M. and Beese, K. (2001) Structural flexibility of the intestine of Burmese python in response to feeding. *J. Exp. Biol.* 204, 325–335
- 28 Levitan, D.R. (1989) Density-dependent size regulation in *Diadema antillarum*: effects on fecundity and survivorship. *Ecology* 70, 1414–1424
- 29 Levitan, D.R. (1991) Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. *Mar. Biol.* 111, 431–435
- 30 Marinovic, B. and Mangel, M. (1999) Krill can shrink as an ecological adaptation to temporarily unfavourable environments. *Ecol. Lett.* 2, 338–343
- 31 Secor, S.M. *et al.* (1994) Rapid upregulation of snake intestine in response to feeding: a new model of intestinal adaptation. *Am. J. Physiol.* 266, G695–G705
- 32 Secor, S.M. and Diamond, J. (1998) A vertebrate model of extreme physiological regulation. *Nature* 395, 659–662
- 33 Madsen, T. and Shine, R. (2001) Do snakes shrink? *Oikos* 92, 187–188
- 34 Palumbi, S.R. (1984) Tactics of acclimation: morphological changes of sponges to an unpredictable environment. *Science* 225, 1478–1480
- 35 Essink, K. *et al.* (1989) On the adaptation of the mussel *Mytilus edulis* L. to different environmental suspended matter concentrations. *Proc. 21st Eur. Mar. Biol. Symp. Gdansk* 1986, 41–51
- 36 Honkoop, P.J.H. *et al.* (2002) Flexibility of size of gills and palps in the Sydney rock oyster *Saccostrea glomerata* (Gould, 1850) and the Pacific oyster *Crassostrea gigas* (Thunberg, 1793). *J. Exp. Mar. Biol. Ecol.* 282, 113–133
- 37 Ebert, T.A. (1996) Adaptive aspects of phenotypic plasticity in echinoderms. *Oceanol. Acta* 19, 347–355
- 38 Fankboner, P.V. and Cameron, J.L. (1985) Seasonal atrophy of the visceral organs in a sea cucumber. *Can. J. Zool.* 63, 2888–2892
- 39 Piersma, T. (2002) Energetic bottlenecks and other design constraints in avian annual cycles. *Integr. Comp. Biol.* 42, 51–67
- 40 Thomas, V.G. (1984) Winter diet and intestinal proportions of rock and willow ptarmigan and sharp-tailed grouse in Ontario. *Can. J. Zool.* 62, 2258–2263
- 41 Starck, J.M. (1999) Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content. *J. Exp. Biol.* 202, 3171–3179
- 42 DeKinga, A. *et al.* (2001) Time course and reversibility of changes in the gizzards of red knots alternately eating hard and soft food. *J. Exp. Biol.* 204, 2167–2173
- 43 Ricklefs, R.E. (1991) Structures and transformations of life histories. *Funct. Ecol.* 5, 174–183
- 44 Murton, R.K. and Westwood, N.J. (1977) *Avian Breeding Cycles*, Clarendon Press
- 45 Jacobs, J.D. and Wingfield, J.C. (2000) Endocrine control of life-cycle stages: a constraint on response to the environment? *Condor* 102, 35–51
- 46 Ricklefs, R.E. and Wikelski, M. (2002) The physiology-life history nexus. *Trends Ecol. Evol.* 17, 462–468
- 47 Montgomerie, R. *et al.* (2001) Dirty ptarmigan: behavioral modification of conspicuous male plumage. *Behav. Ecol.* 12, 429–438
- 48 Levins, R. (1968) *Evolution in Changing Environments*, Princeton University Press
- 49 Moran, N.A. (1992) The evolutionary maintenance of alternative phenotypes. *Am. Nat.* 139, 971–989
- 50 Gwinner, E. (1986) *Circannual Rhythms. Endogenous Annual Clocks in the Organization of Seasonal Processes*, Springer-Verlag
- 51 Wingfield, J.C. and Kenagy, G.J. (1991) Natural regulation of reproductive cycles. In *Vertebrate Endocrinology: Fundamentals and Biomedical Implications* (Vol. 4B) (Schreibman, M. and Jones, R.E., eds) pp. 181–241, Academic Press
- 52 Hoffman, R.J. (1978) Environmental uncertainty and evolution of physiological adaptation in *Colias* butterflies. *Am. Nat.* 112, 999–1015
- 53 De Witt, T.J. *et al.* (1998) Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* 13, 77–81
- 54 Via, S. and Lande, R. (1985) Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39, 505–522
- 55 Gomulkiewicz, R. and Kirkpatrick, M. (1992) Quantitative genetics and the evolution of reaction norms. *Evolution* 46, 390–411
- 56 West-Eberhart, M.J. (1992) Adaptation: current usages. In *Keywords in Evolutionary Biology* (Keller, E.F. and Lloyd, E.A., eds) pp. 13–18, Harvard University Press
- 57 Feder, M.E. and Watt, W.B. (1992) Functional biology of adaptation. In *Genes in Ecology* (Berry, R.J. *et al.*, eds), pp. 365–392, Blackwell Scientific Publications
- 58 Watt, W.B. (2000) Avoiding paradigm-based limits to knowledge of evolution. *Evol. Biol.* 32, 73–96
- 59 Williams, G.C. (1966) *Adaptation and Natural Selection*, Princeton University Press
- 60 Del Hoyo, J. *et al.* (1994) *Handbook of the Birds of the World New World Vultures to Guinea-fowl* (Vol. 2), Lynx Editions
- 61 Levey, D.J. and Karasov, W.R. (1989) Digestive responses of temperate birds switched to fruit or insect diets. *Auk* 106, 675–686
- 62 Krebs, J.R. and Davies, N.B. (1987) *An Introduction to Behavioural Ecology*, Blackwell Scientific Publications
- 63 Piersma, T. *et al.* (1993) Interactions between stomach structure and diet choice in shorebirds. *Auk* 100, 552–564
- 64 Sinervo, B. and Basolo, A.L. (1996) Testing adaptation using phenotypic manipulations. In *Adaptation* (Rose, M.R. and Lauder, G.V., eds) pp. 149–185, Academic Press
- 65 Ketterson, E.D. and Nolan, V. Jr (1999) Adaptation, exaptation, and constraint: a hormonal perspective. *Am. Nat.* 154, S4–S25
- 66 Feder, M.E. *et al.* (1987) *New Directions in Ecological Physiology*, Cambridge University Press
- 67 Feder, M.E. *et al.* (2000) Evolutionary physiology. *Annu. Rev. Ecol. Syst.* 31, 315–341
- 68 Meyers, L.A. and Bull, J.J. (2002) Fighting change with change: adaptive variation in an uncertain world. *Trends Ecol. Evol.* 17, 551–557
- 69 Wikelski, M. *et al.* (1997) Energy limits to body size in a grazing reptile, the Galapagos marine iguana. *Ecology* 78, 2204–2217
- 70 Wikelski, M. and Trillmich, F. (1997) Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* 51, 922–936
- 71 Wikelski, M. and Thom, C. (2000) Marine iguanas shrink to survive El Niño. *Nature* 403, 37
- 72 Lynch, M. and Walsh, B. (1998) *Genetics and Analysis of Quantitative Traits*, Sinauer
- 73 Witte, F. *et al.* (1990) Phenotypic plasticity of anatomical structures and its ecomorphological significance. *Neth. J. Zool.* 40, 278–298
- 74 Dufty, A.M. *et al.* (2002) Hormones, developmental plasticity and adaptation. *Trends Ecol. Evol.* 17, 190–196