

events where the origin and evolution of adaptive phenotypes can be studied directly [7]. Comparative studies may also provide important insights into this process if it can be established that phenotypic accommodation of novel environmental input in ancestral lineages or populations mirrors phylogenetic divergence (e.g. [8–11]).

In conclusion, it seems to us that S&L's notion of genes as 'leaders' or 'followers' in evolution is very different from that discussed in the literature on the evolutionary implications of developmental plasticity, e.g. [2,6–11]. We do not imply that the terminology is better suited for one or the other purpose. However, the move from treating genes as followers when environmental induction initiates evolutionary change, to treating it as a description of the phylogenetic pattern of morph determination, as in S&L, may risk confusing pattern with process. Nevertheless, Schwander and Leimar have provided researchers with a strong incentive for assessing in more detail the developmental regulation of morph expression and its sensitivity to novel input in a comparative context.

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#### Letters Response

## The evolution of novel cues for ancestral phenotypes

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Recent years have seen a growing interest in the role of developmental plasticity in evolution, with issues ranging from adaptive diversification and speciation to the evolution of novel phenotypes [1]. In a recent article in *TREE*, we argued that insights into the importance of plasticity can be gained by inferring transitions between environmental and genetic control of discrete alternative phenotypes [2]. Our approach can reveal whether phenotypes that currently occur as genetic polymorphisms, or as monomorphisms in different populations, were previously elements of reaction norms and, conversely, whether environmentally induced alternative phenotypes derive from genetically controlled variants. We described the two evolutionary sequences as 'plasticity first' and 'genetic polymorphism first' and also labelled them as 'genes as followers' and 'genes as leaders', respectively.

Uller and Helanterä (U&H; [3]) criticise our approach in two ways. First, because we did not address the origin of alternative phenotypes, our approach cannot detect whether phenotypic change originates as environmental induction of novel phenotypes, followed by genetic accommodation. U&H regard this latter process as the major

conceptual alternative to the 'standard view of evolution' [3]. Second, the terminology of 'genes as followers' is only appropriate for such induction–accommodation sequences.

To judge the merits of the criticism, one should ask how helpful the pitting of induction–accommodation sequences against all other forms of evolutionary change is for assessing the importance of plasticity in evolution. We agree that environmental induction of truly novel phenotypes, followed by genetic accommodation, is an interesting process worthy of study. Nevertheless, there are few empirical examples illustrating this process, so perhaps it has a limited role in phenotypic evolution. A broader view of the role of plasticity, that includes cases where already existing phenotypes become induced by novel environmental or genetic cues, might then be preferable. The specific examples that U&H cite in fact suggest that such a broader view is worthwhile. So, in Arizonian house finch populations, adaptive clustering of female versus male offspring along the egg-laying sequence is triggered by mite infestations [4]. Such infestations do not occur in recently colonized northern locations, but sex clustering is induced by exposure to cold temperatures [5]; therefore, the same phenotype is induced by different cues. Phenotypic divergence between spadefoot toad populations might derive from pre-existing developmental and transgenerational

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plasticity [6], or from assimilation of pre-existing plastic responses [7]. The evolution of reduced melanin production in water fleas, as a consequence of the introduction of predatory fish in previously fish-free lakes [8], is likely to be facilitated by an already-present developmental capacity to produce a low-melanin phenotype, and this capacity could be widespread in zooplankton [9,10]. Thus, although each of these examples illustrates the importance of plasticity in evolution, it is uncertain whether new environments induced novel phenotypes.

In our view, these and other case studies would benefit from a phylogenetic perspective on the determination of the studied phenotypes. Such a perspective can reveal which phenotypes and developmental responses existed previously and how they were modified. The phylogenetic pattern is thus of interest even if it cannot demonstrate an underlying process. Our reason for suggesting a focus on discrete alternative phenotypes [2] is that for these, the study of phenotype control and phylogenetic analysis is easier, but we are also in favour of phylogenetic perspectives on continuous reaction norms, whenever these are feasible. Furthermore, we do not disagree with U&H on how shifts in phenotype control can come about (see Box 2 in [2])

Concerning terminology, one could of course restrict the label 'genes as followers' to the possibly rare situations where truly novel phenotypes are induced by (novel) environmental input, but one could also extend the usage of the label to analogous processes where plastic responses precede genetic control [11]. Nothing fundamental hinges on this choice and, at least for our part, we feel that we have not lapsed in defining our usage [2]. Even so, we appreciate the points made by U&H, focusing sharply on the possible importance of induction–accommodation sequences in phenotypic evolution. Our view is that the influence of phenotypic plasticity in evolution is quite significant, but certainly not pervasive, and that the importance of envi-

ronmental induction of truly novel phenotypes might well be small.

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#### Letters

## Optimal diving models: their development and critique requires accurate physiological understanding

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In developing and testing models to predict behaviour, it is important to have sufficient knowledge of the physiological constraints on that behaviour. Although Houston [1] makes several insightful points about the testing of diving optimality models for air-breathers, I argue that some of his criticisms are ill-founded owing to a misunderstanding of relevant metabolic physiology. This serves to underline that quantified physiological understanding and model testing are powerful, sometimes necessary, facets in the development of behavioural optimality models.

Houston [1] criticises the common claim that optimal time allocation of diving behaviour is likely to involve dive durations that approximately reach the aerobic dive limit (ADL). Yet, contrary to the suggestion of Houston [1], this claim is based on theoretical justification; because the ability to gain oxygen while at the surface is subject to diminishing returns [2,3], the time to take up a given amount of oxygen is reduced by returning to the surface with only a small amount of available oxygen remaining.

The ADL was coined as the dive duration at which post-dive blood lactate concentration increases [4] and this

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