

will only lead to the discovery of plasticity genes by chance, or after exhaustive effort.

The study of plasticity, and of plasticity genes, will be important and useful for our understanding of the response of organisms to the environment. At this early stage, where evidence is being drawn together from molecular, physiological, evolutionary and ecological research, we need to define clearly what we are hoping to explain and to be realistic about expectations for the results of our experiments.

### Jamie S. Day

Dept of Biochemistry, University of Otago, PO Box 56, Dunedin, New Zealand (jamie@sanger.otago.ac.nz)

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### Reply from M. Pigliucci

Day's letter offers me an opportunity to clarify a few points about the genetics of plasticity.

(1) Definition of plasticity: the ambiguity in the current definition of plasticity reflects an ongoing debate in the field. My personal preference is to limit the term to developmentally based morphological or life history changes. However, many physiological, as well as behavioral, traits certainly present a striking similarity to plasticity – they can be studied by using analogous methods, and they possibly reflect a more general class of biological phenomena.

(2) Environmental stimuli: I would definitely not include endogenous stimuli among the stimuli to which an organism displays plasticity. Again, this is currently a matter of debate, and it may reflect a deeper commonality of which we should be aware. However, I think that this restriction is adopted by the majority of researchers in the field, and that it reflects an objective distinction between external and internal environments.

(3) Specific series of morphological changes: the distinction between 'labile' and 'fixed' plastic responses matches fairly closely the distinction between physiological and developmental plasticity. Maybe we should simply use these last two terms (together with the analogous behavioral plasticity, since not all behaviors are 'plastic') in order to clarify what the object of study is in each particular case.

(4) Plasticity genes: at the risk of appearing to repeat the same argument, this is also a matter of discussion and – to some extent – personal preference. I rather consider plasticity genes to be those elements that Day refers to as 'receptors' (of environmental stimuli), such as the phytochromes (here, though the gene's expression is not altered by the environment, the state of the protein is). However, it has to be clear that the study of the genetic basis of plasticity implies a lot more than just plasticity genes. For example, the transduction elements to which Day alludes must certainly be included. The special status of plasticity genes comes from the fact that it is particularly intriguing to consider how they came to evolve, since they do not make sense within single

environments, thereby implying direct selection for the existence of a plastic response (*contra* Via<sup>1</sup>; see Schlichting and Pigliucci<sup>2</sup>). I do agree with Day that the genetic analysis of plastic reactions may be complex and sometimes impossible. I believe, however, that recent successes and the evolutionary importance of evolution in response to environmental heterogeneity make it a worthy challenge for any researcher so inclined.

### Massimo Pigliucci

Depts of Botany and of Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN, USA

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### Liver physiology and sex ratio biology

Godfray and Werren<sup>1</sup> admirably summarize the impressive increase in our understanding of the ecology and evolution of sex ratios in organisms ranging from protozoa to birds. Imagine my concern when they singled out my views<sup>2</sup> on this subject and described them as being 'jaundiced'. Consulting my dictionary, I found out that I was either 'affected with or colored by or as by jaundice' or 'affected with or exhibiting prejudice, often resulting from a particular experience, social position, etc.' I rushed off to get another opinion. But my internist could find nothing wrong and my psychiatrist came up with nothing either (much to the surprise of my friends!). Perhaps something else is going on, I was told. A friend asked, could it be that I simply have a different view of sex ratio biology, especially in parasitic wasps, a view that acknowledges the present knowns as well as emphasizes the substantial unknowns? Perhaps, perhaps not, I thought.

Seeking further clues, I went to the library and discovered that Godfray had previously stated<sup>3</sup> that my co-worker and I 'misunderstand' behavioral ecology and that I have used our experimental results to 'mount an angry attack' on the field. Imagine my surprise. After all, my co-worker and I had produced an extensive set of experimental results relating to sex ratio biology in a parasitic wasp<sup>4–10</sup>. For example, by the use of genetic markers, we produced the *only* analysis of the sex ratio behavior of individual females in multi-female foundress groups<sup>9</sup> and showed that there is qualitative and quantitative heterogeneity of fit of behaviors to the predictions of well-motivated optimality models. Such information on the traits manifested by an individual (as opposed to groups of individuals) is essential for making claims for or against optimality, as the causal basis of such models is that the trait of an individual has a higher fitness than those of other individuals. We were also the first to describe genetic variation for sex ratio traits within local populations. All of these results indicate that there is no present basis for a claim of optimality for these traits in this species, as had been claimed previously without information about the behaviors of individuals. Instead, it may be

that genetics has 'gotten in the way' of the evolution of optimal traits in these instances. Of course, such an assertion needs to be tested. In any case, such results have general implications for the testing of optimality models and for our understanding of the meaning and testability of adaptationism<sup>11–13</sup>. For example, it appears that these studies are just one of two sets of studies of any kind of trait in the literature in which the nature of the data and of the analyses allows a proper assessment of the local optimality of the trait<sup>11</sup>. Or so I thought. To be sure, if we failed to understand behavioral ecology, all of our work would be meaningless. I guess I'm confused...

Of course, there is a serious point to all of this, beyond having fun. Only careful experiments, critical analyses of data and of models, and recognition of the substantial gaps in our knowledge (such as the fact that there are no *data* on population subdivision in almost all species for which it is claimed that subdivision drives the evolution of female-biased sex ratios) will advance our understanding of sex ratio evolution. All else serves another purpose.

### Steven Orzack

Fresh Pond Research Institute, 64 Fairfield Street, Cambridge, MA 02140, USA and Dept of Ecology and Evolution, University of Chicago, 1101 E. 57th Street, Chicago, IL 60637, USA

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### Reply from H.C.J. Godfray and J.H. Werren

We are very sorry for driving Steven Orzack to consult his physician and psychiatrist; delighted that he should obtain a clean bill of health; and far too polite to suggest that he should get a second opinion. Our dictionary gives a slightly different definition of jaundiced, a 'disposition to take an

unfavourable view', and we used the word in this sense as the mildest of hepatic metaphors (as opposed to, say, liverish or bilious). In our opinion, Orzack's oft-stated philosophical views on optimality theory have influenced his interpretation of sex ratio data, a charge he has levelled at others. But we firmly believe that the subject benefits from a diversity of views, each stoutly defended. Indeed, the offending sentence in our article was expressly intended to alert the reader to an alternative view of sex ratio evolution.

#### H.C.J. Godfray

Dept of Pure and Applied Biology,  
Imperial College at Silwood Park,  
Ascot, UK SL5 7PY

#### J.H. Werren

Dept of Biology, University of Rochester,  
Rochester, NY 14627, USA

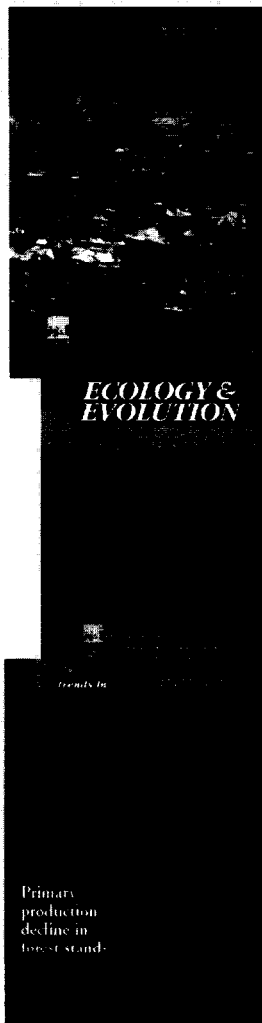
### Value in biodiversity, ecological services and consensus

In his recent *TREE* article<sup>1</sup>, Charles Perrings claims that there is now a consensus that 'The main value of biodiversity...is...derived from the role of a combination of species in supporting specific ecological services'. While we agree that ecological services are among the biological phenomena that are most highly valued by people, we disagree that this can necessarily be equated with the value of biological *diversity* in a strict sense.

Perrings distinguishes carefully between the value of individual biological resources and the value of biodiversity. Yet he points out that highly valued ecological services may, in fact, be provided by *low diversity* assemblages of organisms. There is no redeeming implication that the organisms in these valued assemblages are particularly different or unusual, for example, in the sense of being particularly genetically, morphologically, behaviourally, or even 'functionally', divergent, either from one another or from organisms in other assemblages. In contrast, we consider the most widely held value of *biodiversity* to reside in the variety of expressed genes or characters among organisms<sup>2,3</sup>. This constitutes something rather different from the ecological services that assemblages of organisms provide.

The problem is that the term biodiversity has come to mean a diversity of things to a diversity of people<sup>4</sup>. But if it is not to become a meaningless synonym for 'all life', then ideally it should be reserved for the sense of richness in the variety of different biological entities. Ecological services should be valued highly, and possibly most highly, but should not be conflated with biodiversity<sup>5</sup>. That others support this view would seem to be confirmed by the existence of a literature explicitly exploring how variation in diversity influences provision of services<sup>6,7</sup>.

We appreciate that a consensus on values is important for achieving conservation action. We hope that by attempting to reduce opportunities for misunderstandings, the consensus (and perhaps greater biodiversity) is more likely to survive.



## trends in **ECOLOGY & EVOLUTION**

### Coming soon in *TREE*:

The population genetic consequences of habitat fragmentation for plants, *A. Young et al.*

The dynamics of operational sex ratios and competition for mates, *C. Kvarnemo and I. Ahnesjö*

Niche versus chance and the diversity of tropical trees, *N.V. Brokaw*

Patterns in the distribution and abundance of grassland species, *S. Naeem*

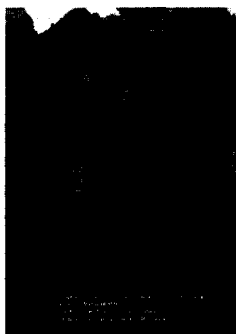
Individual-based modelling in ecology: what makes the difference? *J. Uchmanski and V. Grimm*

Ecological and conservation insights from reconstructive studies of temperate old-growth forests, *D.R. Foster et al.*

Restoration ecology: science, technology and society, *N.R. Webb*

Microsatellites, from molecules to populations and back, *P. Jarne and P.J.L. Lagoda*

Reintroduction: challenges and lessons for basic ecology, *F. Sarrazin and R. Barbault*



### **TREE** cover competition

The cover of the June issue of *TREE* was a view of Cradle Mountain, Tasmania. A single correct answer was received: the winner was J. Read, of Monash University, Australia, who wins a free subscription to *TREE*. No other entrant even identified the continent correctly, though all were restricted to the Old World, including sites in Europe, Africa and India.

**Paul Williams  
Chris Humphries  
Dick Vane-Wright**

Biogeography and Conservation Lab,  
The Natural History Museum,  
Cromwell Road, London, UK SW7 5BD

**Kevin Gaston**

Dept of Animal and Plant Sciences,  
University of Sheffield, Sheffield,  
UK S10 2TN

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