Book Review

Life without purpose

Not by Design: Retiring Darwin's Watchmaker by J.O. Reiss. University of California Press, 2009. £34.95 hbk (440 pages) ISBN 978 0 520 25893 8.

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Biologists have a love–hate relationship with teleology. On the one hand, we can (in principle) explain all of biology from a purely material perspective, without recourse to final causes. On the other hand, apparent purposefulness is the defining quality of life, and even the technical discourse of the biological sciences is shot through with the language of intentionality: function, optimum, conflicts of interest, selfishness, altruism. This tension is particularly tangible in my own research area, which occupies the overlap between theoretical population genetics (in which teleology is anathema) and behavioural ecology (in which the analogy of purpose is the paradigm). Seeking to confront this basic contradiction, John O. Reiss, in *Not By Design: Retiring Darwin's Watchmaker*, looks to history in order to discover the origins of the dilemma, as well as a possible resolution. He concludes that we must totally purge the analogy of teleology – and associated intentional language – from evolutionary biology.

In the first part of the book, Reiss takes us on a fascinating historical tour of the teleology controversy in pre-Darwinian thought. The original players, insofar as history has been able to record, were the ancient Greeks. Embracing teleology is the master philosopher Socrates (c. 496–399 BC), whom Xenophon records as musing upon the inherent purposefulness of morphological and behavioural adaptations wielded by animals. Denying teleology is the shamanic Empedocles (c. 490–430 BC), whose poetry describes a time of random explosion in organism diversity ("as many heads without necks sprouted up/and arms wandered naked, bereft of shoulders/and eyes roamed alone, impoverished of foreheads") followed by a period of winnowing whereby the more awkward permutations perished. Reiss traces these opposing philosophical strands as they pass, curiously unaltered, out of the classical era, through the dark ages and the Renaissance, to the early 19th century. Here, they find their expression in the writings of William Paley (1743–1805) and Georges Cuvier (1743–1832). Whilst Paley proclaims the adaptation of organisms the greatest evidence for a divine creator, Cuvier regards adaptation as a necessary condition for the organism to exist and hence – applying a biological variant of the weak-anthropic principle – finds the adaptation of (existing) organisms a phenomenon requiring no further explanation.

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The book then moves on to cover Darwinism, and to question its place in current evolutionary biology. Reiss argues (correctly, in my view [1]) that Darwin's intellectual genealogy lies more with Paley than with the Cuvierian tradition. Having allied Darwin with the teleologists, Reiss unveils his plan of action: first, he will demolish the analogy of teleology in biology, by breaking the link between natural selection and design; second, he will exorcise the spectre of teleology by rejecting Darwinism altogether, and rebuilding biology upon a Cuvierian bedrock. This is excitingly ambitious, and the reader appears to be in for a treat. Unfortunately, Reiss spends the remainder of the book lambasting a form of teleology to which no respectable biologist subscribes. And whilst his proposed alternative conception of evolutionary theory may be philosophically sound, it falls staggeringly short of replacing the Darwinian view of adaptation by natural selection.

Reiss's conception of 'good design' in biology turns out to be a population's ecological success, i.e. continued existence (p282). He labours to show that natural selection does not always drive populations in the direction of good design (defined in this way), and hence rejects the notion of purpose in evolution altogether. However, what Reiss has actually disproved is the now thoroughly-discredited group adaptationism of Wynne-Edwards [2]. Other flavours of teleology are available, and the standard approach is to view design as occurring at the level of the individual organism, where it functions to maximise the individual's inclusive fitness [3]. The formal correspondence between the dynamics of natural selection and this more standard view of phenotype design is well established [4,5]. Hence, there is nothing wrong with a little teleology in the biological sciences: the proposed retirement of Darwin's watchmaker is an unfair dismissal.

Teleology aside, Reiss's alternative to Darwinism is simply not up to the job. Whilst it is true that organisms can be expected to display some adaptation, by virtue of their very existence, Cuvier's principle does not explain the origin of adaptation, i.e. why we see adapted organisms rather than no organisms. Darwin's genius was to emphasise the individual organism as the unit of reproduction and heredity. Thus, we can explain how adaptation is built up, cumulatively, over generations, driven by competition between individual organisms. Whilst Cuvier's approach is to deny the problem of adaptation, Darwin's is to provide a proper solution, which illuminates the origin of biological design, as well as its purpose.

References

1 Gardner, A. (2009) Adaptation as organism design. *Biol. Letts* 5, 861–864
2 Wynne-Edwards, V.C. (1962) *Animal Dispersion in Relation to Social Behaviour*, Oliver & Boyd
3 Hamilton, W.D. (1964) The genetical evolution of social behaviour I & II. *J. Theor. Biol.* 7, 1–52 DOI: 10.1016/0022-5193(64)90038-4
4 Grafen, A. (2002) A first formal link between the Price equation and an optimization program. *J. Theor. Biol.* 217, 75–91 DOI: 10.1006/yjtbi.3015
5 Grafen, A. (2006) Optimization of inclusive fitness. *J. Theor. Biol.* 238, 541–563 DOI: 10.1016/j.jtbi.2005.06.009

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Book Review

Towards a better understanding of life

Phenotypic Plasticity of Insects: Mechanisms & Consequences by Douglas W. Whitman and T.N. Ananthakrishnan. Science Publishers, 2009. US$135.00 hbk (904 pages) ISBN 978-1-57808–423-4

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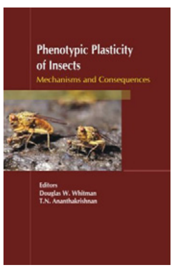

A grasshopper finds itself constantly bumping into other grasshoppers. Consequently, when she lays her eggs, she puts a chemical in the egg foam that induces the developing brood to be sociable and to develop a bright warning coloration. They brood will grow up to be quite distinct and unlike their unfriendly, cryptically-colored parents. Inchworm caterpillars that feed on oak catkins take on the appearance of oak catkins, in contrast to their oak-leaf eating, oak-leaf mimicking siblings. These remarkable examples of phenotypic plasticity in insects are two of the myriad case studies used in this volume to present the significance of the potential for a single genotype to exhibit a range of phenotypes in response to environmental variation. According to Whitman and Ananthakrishnan, understanding phenotypic plasticity will lead to a 'better understanding of life.'

Phenotypic plasticity has enjoyed a modicum of popularity in evolutionary biology in the last decade. Many reviews and books have been published that alert the savvy evolutionary biologist to the primacy of phenotypic plasticity in evolutionary biology and its pervasiveness in all biological disciplines (for two influential reviews see [1,2]). The unifying paradigm among all of these works is that a phenotype is a complicated product of gene (nature) by environment (nurture) interactions and that variation is the rule and not the exception. Whitman & Ananthakrishnan not only present an anthology of many of the most striking examples of insect polyphenisms and polymorphisms, but also several unique perspectives on the origins of phenotypic plasticities and the evolvability of plastic phenotypes.

This collection of papers opens with a comprehensive overview, defining and justifying phenotypic plasticity, and comes complete with a glossary at the end. This is followed by an historical review and current perspectives chapter. These two chapters attempt to standardize the terminology in the field (although it seems they did not pass this information along to the other contributors since there are many different usages of the terms polymorphism and polyphenisms throughout the volume). The subsequent chapters include many of the standard case studies of phenotypic plasticity in insects, such as polyphenic horned and hornless beetles, polyphenic geometrid caterpillars, phase polyphenic locusts, polyphenic butterflies, wing-polymorphic crickets, and seed beetles that exhibit plasticity in egg size. These insect examples are well known and have been written about in other reviews of phenotypic plasticity; for example, Mary Jane West-Eberhard published what one reviewer has called a 'milestone classic of epic proportion' with her book *Developmental Plasticity and Evolution* [2,3], which provides a synthetic and comprehensive treatment of phenotypic plasticity with examples from all spheres of life encompassing evolution, development, and behavior. However, having a compilation of reviews of these biological systems written by the principle researchers and pioneers in the field is a truly valuable contribution. There are several additional examples included that are perhaps not known as phenotypic plasticities *per se*, but are worth mentioning because they are interesting and a bit different. These include density-dependent prophylaxis, natural enemy induced plasticity, body size plasticity in yellow dung flies, plasticity in homeostatic physiological systems, and physiological phenotypic plasticity or acclimation. The other chapters stand out for the uniqueness of their approaches and perspectives. For example, one chapter uses a biophysical model of temperature-dependent biological rates to describe phenotypic plasticity in insect development rates, growth rates, and body size. Although no discussion of phenotypic plasticity is complete without a discussion of canalization, interestingly, this chapter describes how heat shock proteins not only limit alternative phenotypes but also maintain and permit phenotypic plasticity in several different biological systems.

Overall, this book is an excellent new resource and anthology of case studies of phenotypic plasticity in insects, incorporating both mechanisms and consequences. In addition, it provides new perspectives on the origins,

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