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## Organisms, Agency, and Evolution

The central insight of Darwin's *Origin of Species* is that evolution is an ecological phenomenon, arising from the activities of organisms in the 'struggle for life'. By contrast, the Modern Synthesis theory of evolution, that rose to prominence in the twentieth century, presents evolution as a fundamentally molecular phenomenon, occurring in populations of suborganismal entities – genes. After nearly a century of success, the Modern Synthesis theory is now being challenged by empirical advances in the study of organismal development and inheritance. In this important study, D.M. Walsh shows that the principal defect of the Modern Synthesis resides in its rejection of Darwin's organismal perspective, and argues for 'situated Darwinism': an alternative, organism-centred conception of evolution that prioritises organisms as adaptive agents. His book will be of interest to scholars and advanced students of evolutionary biology and the philosophy of biology.

D.M. WALSH is Professor in the Department of Philosophy, the Institute for the History and Philosophy of Science and Technology, and the Department of Ecology and Evolutionary Biology at the University of Toronto. He is the editor of *Naturalism, Evolution and Mind* (Cambridge, 2001) and the coeditor of *Evolutionary Biology: Conceptual, Ethical and Religious Issues* (with R. Paul Thompson, Cambridge, 2014).

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For Margaret O'Malley

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## Contents

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<i>Preface</i>	<i>page ix</i>
Introducing organisms: between unificationism and exceptionalism	1
<b>Part I: The eclipse of the organism</b>	21
1 Mechanism, reduction and emergence: of molecules and method	25
2 Ensemble thinking: of struggle and abstraction	43
3 The fractionation of evolution: struggling or replicating?	65
<b>Part II: Beyond replicator biology</b>	87
4 Inheritance: transmission or resemblance?	91
5 Units of phenotypic control: parity or privilege?	114
6 Fit and diversity: from competition to complementarity	133
7 Integrating development: three grades of ontogenetic commitment	150
<b>Part III: Situated Darwinism</b>	163
8 Adaptation: environments and affordances	167
9 Natural purposes: mechanism and teleology	186
10 Object and agent: enacting evolution	208
11 Two neo-Darwinisms: fractionated or situated?	230
<i>References</i>	248
<i>Index</i>	275
	vii

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## Preface

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When I took my first ethology course, I was instructed to make an ethogram. An ethogram is a catalogue of the movements, postures and sounds of a target organism whose behaviour one wishes to study. The objective of the ethogram is to free the observation of behaviour from any taint of purpose or intention. We were to identify behaviours with manifestations, rather than motives. I was told that my Columbian Ground Squirrels (*Spermophilus columbianus*) were standing on their hind legs at full height, rather than surveying the scene for predators. They were emitting a high-pitched ‘bark’, rather than alerting their fellow colony members to imminent dangers. As a biddable undergraduate, I dutifully went along with this, even though I could see that my squirrels were looking for something, and warning each other. My brush with ethology taught me three things. The first is that midnight black is the best hair-dye tint for painting patterns on ground squirrels. The other two are less practical. They are that organisms are fundamentally purposive entities, and that biologists have an animadversion to purpose. These perplex me: why should the phenomenon that demarcates the domain of biology be off-limits to biology?

This is more than just an idiosyncratic bemusement on my part. It is a *leitmotif* that runs through the entire history of biology. Since its inception, biology seems to have been torn by the evidently incompatible demands of treating organisms as natural entities, like everything else, and as singularly peculiar (naturally purposive) things, unlike anything else. One of the common strategies has been to attempt to minimise the distinctiveness of organisms, to show that the problematic nature of organisms is incidental to a comprehensive understanding of understanding of biology, and that the principles by which we account for nonliving phenomena are wholly adequate to the explanation of living phenomena. This is a bold move, and it is fair to say that it has paid dividends.

Nowhere is it pursued more vigorously, or more successfully, than in the theory of evolution that descended from Darwin’s and grew to prominence throughout the twentieth century. The Modern Synthesis theory of evolution is elegant and powerful. Inspired by the molecular revolution in biology, the Modern Synthesis circumvents the ‘organism’ issue by making genes the

canonical unit of biological organisation. Modern Synthesis evolution is a fundamentally molecular phenomenon. It is the process in which a giant molecule, DNA, is replicated, and transmitted from one generation to the next, whereupon it builds entities ('vehicles' or 'interactors') that help to spread further replicates.

No one can gainsay the advances in our understanding of biology ushered in by the Modern Synthesis. It is now coming up for a century of unparalleled success. But we are beginning to see intimations that, perhaps, this disorganised evolutionary thinking may be running up against its limitations. These deficiencies, by my reckoning, occur at just the places where our understanding of evolution could be enhanced by paying attention to the contribution of organisms *as* organisms.

Whether or not the Modern Synthesis is reaching the end of its useful life, there is ample justification for exploring an alternative. It lies in the fact that Modern Synthesis thinking misrepresents the metaphysics of evolution. Evolution, properly construed, is not so much a molecular phenomenon as an ecological one. It arises out of what organisms do in the pursuit of their ways of life. That, I take it, is the lesson of cardinal importance to be drawn from Darwin's *Origin of Species*. But it is precisely this perspective that has been obscured by the marginalisation of organisms that has taken hold under the Modern Synthesis. I think it is a salutary exercise to contemplate what we might have missed by leaving organisms out of our understanding of evolution. That is the objective of this book.

The book comprises three main parts. Part I, 'The Eclipse of the Organism', is my attempt to explore some of the reasons behind the peripheralisation of organisms in Modern Synthesis evolutionary biology. They are, as the ecologists say, 'complex and interacting'. I have chosen to tease apart (as the anatomists say), and concentrate on, three: methodological, theoretical and empirical. After an introductory chapter that attempts to motivate the problem that organisms pose for the understanding of evolution, I proceed to make the case. Chapter 1 argues that Modern Synthesis biology has embraced the precepts and procedures of mechanism. This is hardly surprising, as mechanism is the methodological standard under which the startling advance of modern sciences has marched. Be that as it may, mechanism appears to be ill-suited to the task of capturing the distinctive features of organisms. In Chapter 2, I explore the way that the specific kind of population thinking ushered in at the inception of the Modern Synthesis leaves the (erroneous) impression that there is no room for organisms in evolutionary dynamics. Our current theory of population change gives us ensembles of abstract entities – gene types – and the forces that propel them around genotype space, but there are no organisms in its ontology. One is invited to suppose that, to the extent that this theory is adequate, organisms are redundant to theoretical biology.

Chapter 3 explores the consequences of the discovery and intensive concentration on genes that has inspired the growth of twentieth-century biology (and continues to do so). The gene has encouraged what I call the ‘fractionation’ of evolution. Thanks to gene centrism we can think of the component processes of evolution – inheritance, development, adaptive change and the origin of novelties – as discrete and autonomous. Together, they comprise evolution. They are united by the fact that the gene is the canonical unit in the explanation of each process.

Fractionation, I think, is the linchpin of Modern Synthesis, gene-centred thinking. It is what undergirds the Modern Synthesis approach to evolution that I call Replicator Biology. If fractionation is right, I reckon, so is Replicator Biology. Fractionation amounts to the great empirical wager of the Modern Synthesis. While fractionation is not usually the explicit target of those who wish to challenge the Modern Synthesis, it is the implications of fractionation that have been most vigorously opposed in recent evolutionary biology and its philosophy.

Part II, ‘Beyond Replicator Biology’, explores the ways that recent advances in our understanding the processes of inheritance, development and the production of evolutionary novelties challenge the fractionated picture of evolution. Chapter 4 argues that the Modern Synthesis mischaracterises inheritance. For the purposes of understanding evolution, inheritance should be construed as a gross pattern of intergenerational resemblances and differences. Instead it has been recast as the process in which genetic material is replicated and transmitted from parent to offspring. But the process of transmission isn’t adequate to capture all that is evolutionarily important about the pattern of inheritance. In its place, I offer in outline a conception I call ‘inheritance holism’. Chapter 5 discusses the Modern Synthesis conviction that genes are units of phenotypic control. The appeal of this picture is lent a considerable degree of support by the much maligned ‘information’ or ‘genetic program’ metaphor. While I find the standard battery of arguments against the ‘genetic information’ or ‘genetic program’ programme inconclusive, I offer a new one that I believe successfully undermines the presumptive privilege of genes in development. Here again, I argue that genes are generally not units of phenotype control; organisms are. Chapter 6 addresses what I take to be a deep conceptual confusion concerning the relation between natural selection and organismal development in current evolutionary thinking. Typically, the process of development is pitted against the process of selection, as a competing evolutionary force. Selection, the force, is the source of adaptive bias in evolutionary change, whereas development is fundamentally conservative. This, I argue, is a misconstrual of both the process of selection and development. Chapter 7 seeks to rectify it. Rather than the replication and transmission of genes as the unifying processes in evolution, I propose that organismal development (broadly construed) is. Evolution, I maintain, is development writ large.

Part III lays the conceptual foundations of an organism-centred alternative to Modern Synthesis thinking that I call ‘Situated Darwinism’. Situated Darwinism is an account of how evolution falls out as a consequence of organisms’ purposeful pursuit of their ways of life. The central guiding idea is that organisms are adaptively engaged in what I call, borrowing a term from ecological psychology, their system of ‘affordances’. This perspective requires a significant amount of conceptual retooling. Chapter 8 argues that the Modern Synthesis theory has comprehensively misrepresented one of its principal explananda, adaptation. Adaptation, I argue, should be seen as a response to affordances, and not to external environments. The notion of affordance crucially implies purpose. If affordances figure in evolution, then so do purposes. In Chapter 9 I claim that the principal impediment to generating a comprehensive alternative to the Modern Synthesis has been the modern antipathy to natural purpose. I argue that our post-Scientific Revolution deteleologised worldview has conspired against the inclusion of organisms in evolution. Chapter 10 asserts that this purposive perspective cannot just be grafted onto the Modern Synthesis theory. The reason is that organisms participate in evolution as agents. In order to accommodate this fact we need a special kind of theory, that I call an ‘agent theory’. The Modern Synthesis is an ‘object’ theory. Agents do not figure *as agents* in object theories. So the Modern Synthesis cannot simply assimilate the organismal perspective as an add-on. Chapter 11 draws together the various strands of the preceding discussion in order to give a more explicit expression of this alternative ‘Situated Darwinism’. It compares the conceptual underpinning of this nascent view of evolution with those of the more traditional Modern Synthesis. It illustrates the various ways in which organisms, as purposive agents, contribute to – indeed *enact* – evolution. The result is a way of thinking about evolution that is somewhat at variance with the orthodox Modern Synthesis.

I make only minor apologies for not saying much in what follows about how this conception of evolution might alter the way biologists approach the empirical investigation of evolution. I wish I could say more, but I feel both that I can’t, and that even if I could I shouldn’t. I have refrained in part because my interests lie more in understanding the metaphysics of evolution – what happens when evolution happens – than in how to study what happens when evolution happens. Mostly, I have demurred because it is presumptuous for a nonpracticing biologist to tell biologists how to go about their business. I have neither the expertise nor the hubris even to attempt that. I do, however, find myself sufficiently in awe of the ingenuity of practicing scientists to believe that if this way of thinking about evolution is viable and calls for a new way of studying it, biologists will be able to devise appropriate methods and procedures. My guess, if I were to venture one, would be that less change needs to be made to biologists’ practices than to our interpretations of their findings.

Nor do I say much in what follows about the individuation of organisms. This, too, is a difficult issue, one that has generated an impressive philosophical literature, but not a great deal of consensus. There may be no general agreement on what an organism is, but there is, nevertheless, a reasonable degree of agreement on which things are organisms. That is sufficient for my purposes. All organisms, from the most rudimentary to the most complex, manifestly possess the capacities – plasticity, robustness, purposiveness – that, I maintain, make them agents of evolution.

I should say a word about my intended audience: there isn't one. (That may turn out to be prescient.) I would hope that this material is of interest to philosophers and evolutionary biologists alike, and even to historians of science. I think these considerations may also be relevant to those working in the philosophies of action and mind, and in naturalised meta-ethics. In what follows I haven't presupposed any particular expertise in any of these disciplines, in the hope that it may be accessible to practitioners in all these fields.

I started formulating the view I present here some time ago, during a short sabbatical spent as a guest of Richard Lewontin at Harvard University. I am happy to acknowledge my deep debts to him. One of my motivations in preparing this work has been to try to come to grips with Lewontin's repeated call for biologists and philosophers to revise the way we think of organisms in relation to their environments. This is the kernel of my enjoinder that we should understand organisms as agents embedded in a system of affordances. I hope I have made some progress toward the revision he has in mind.

I was delighted when Michael Ruse invited me to commit my perplexity to paper for his Cambridge Philosophy of Biology series. Little was he to know how deep my puzzlement ran or how widely it would ramify, nor was I for that matter. The exercise has been an education for me. The result is a little bit late to say the least, but here it is. I am extremely grateful to Michael for his steadfast encouragement, even through long stretches of time in which it looked as though no manuscript would ever materialise. I am also grateful to Hilary Gaskin at Cambridge University Press for her forbearance.

The old proverb says it takes a village to write a book. I'm privileged that my village is peopled by such fine, gentle folk, and really smart too – in fact, I usually feel like its idiot. It comprises teachers, students, colleagues and family. I acknowledge their help and support, and I am greatly obliged to them all. Richard C. Fox, Robert L. Carroll, Mark Sainsbury, David Papineau and Farish Jenkins have all taught me with patience and kindness. I reserve special thanks in this regard for Elliott Sober. My own move from biology to philosophy was largely inspired by Elliott. He later became my mentor in the field. My debt to him is inestimable. He is not to be held responsible, of course, for my having gone off course.

I have had the honour of working with wonderful students: Rachel Bryant, Michael Cournoyea, Alex Djedovic, Eugene Earnshaw-Whyte, Fermin Fulda,

Cory Lewis, Parisa Moosavi. It is a terrific thrill to be challenged by such acute minds. They have all helped me to refine and extend my thinking in myriad ways. Mike Stuart taught me about vitalism. Cory Lewis and Alex Djedovic each read through the entire penultimate draft of the entire manuscript and offered me extremely helpful advice. Without their astute critiques the final result would be, well, a lot worse. I have had terrific colleagues over the years who have given me help, support and inspiration. I'm indebted to Alexander Bird, Anjan Chakravartty, Philippe Huneman, Mohan Matthen, Mark Solovey, Larry Shapiro, Jacob Stegenga and Marga Vicedo. I should single out André Ariew, from whom I have learned so much. And there is family. Deborah Kohn has given her loyalty and love selflessly, even to the extent of surrendering her comfy wicker chair to the cause of philosophy. Aoiffe and Lia are both both a wonder and a joy. There are even mothers: Margaret Mary O'Malley and Dr V.L. Kohn. Sadly, since this manuscript was submitted for publication, Dr Kohn died. I do wish to express my admiration for her, and acknowledge my debt to her.

I began writing this manuscript while a visiting scholar at the KLI institute for the Study for Natural Complex Systems. In fact most of the first version was written during various sojourns there over the years (first in Altenberg, then in Klösterneburg, Austria). I am extremely grateful to my friends at the KLI for offering such a convivial and productive atmosphere. I would particularly like to mention Gerd Müller, Werner Callebaut, Isabella Sarto-Jackson and Eva Kärner in this regard. Sadly, our community lost Werner Callebaut, again during the short time between the submission of this manuscript and its publication. The loss to philosophy of biology is difficult to fathom. I am grateful to LaMancha Hub in the Scottish Borders and the public libraries in Toronto; Chagrin Falls, Ohio; and Ellsworth, Maine, for providing me with spaces to work. I am particularly grateful to David Depew and Jonathan Kaplan, both of whom read the penultimate version of the manuscript and provided wonderfully insightful comments.

Despite the efforts of all these good people, inaccuracies, infelicities, incomprehensibilities, heterodoxies, heresies and howlers remain. These are all my own work. Together (with whatever good bits), they make up my attempt to deal with the conundrum of organisms in evolution. If you read on you will be asked to entertain the idea that organisms are agents of a sort – not cognitive agents, but natural purposive systems nevertheless – and through this agency they enact evolution. Moreover, assimilating the agency of organisms into evolutionary thinking renders a conception of evolution that, while wholly consistent with Darwinism, puts considerable strains on the Modern Synthesis account of evolution with which we have all become so comfortably familiar. I can imagine that this message might not go down so smoothly with all readers. Never mind; I can always go back to painting squirrels.