Russell, Edward Stuart

Advanced article

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Edward Stuart Russell (1887–1954) was a central figure in the philosophy of biology during the first half of the twentieth century. Although he worked as a government fisheries scientist for much of his life, he still managed to establish himself as one of the most prominent biological theorists of his time. The views he developed, which were antireductionistic, organism-centred, and teleological, challenged the prevailing mechanistic orthodoxy. His book *The Interpretation of Development and Heredity* (1930) provides one of the most incisive critiques of the chromosomal theory of the gene ever published, and it has acquired a renewed relevance in light of recent empirical findings. Russell's interest in the theoretical problems of biology is as much historical as philosophical, and many of his works, particularly his first book *Form and Function* (1916), are still regarded today as landmark contributions to the history of biological thought.

Edward Stuart Russell (**Figure 1**) was born near Glasgow, Scotland in 1887. He entered the University of Glasgow in 1904 to study arts and sciences, earning a MA in 1907 and a BSc in 1909. He developed an interest in marine biology as a student of Graham Kerr, and after graduating he came under the influence of J. Arthur Thompson and Patrick Geddes. In 1909, he became an inspector for the Board of Agriculture and Fisheries, moving to London and eventually rising to the position of director of fisheries investigations in 1921 in the Ministry of Agriculture and Fisheries. In 1930 he was awarded an OBE for his contributions to fisheries research. He was the first editor of the *Journal du Conseil* (now *ICES Journal of Marine Science*) from 1926 to 1940, and he was a council member of the Marine Biological Association between 1927 and 1943. He served as president of the zoology section of the British Association for the Advancement of Science (BAAS) in 1934 and as president of the Linnean Society between 1940 and 1942. He retired in 1947, having spent 37 years as a civil servant.

Russell's most lasting impact on fisheries research was his adoption of quantitative methods for gathering fisheries data. In 1931 he published an influential paper on the problem of overfishing, in which he presented a simple equation that took account of the various factors that influenced fish yields (Russell, 1931). In 1939 he was invited by Raymond Pearl to deliver a series of lectures on this topic at Johns Hopkins University. These were published a few years later as *The Overfishing Problem* (1942). Russell also lectured regularly on animal behaviour at University College London between 1932 and 1947. *The Behaviour of Animals: An Introduction to Its Study* (1934a) is based on the lectures he gave in 1933. Animal behaviour was also the subject of his presidential addresses to the BAAS (Russell, 1934b) and to the Linnean Society (Russell, 1941, 1943, 1944). He even published an article in which he interpreted his own observations of his pet dog—a Fox Terrier called Gina (Russell, 1936a).

Still, it is not as a fisheries scientist that Russell is primarily remembered today, but as a historian and philosopher of biology. His remarkable contributions to these fields are what makes Russell such a notable figure of early twentieth-century biology. His most well-known work is his first book, *Form and Function: A Contribution to the History of Animal Morphology* (1916a), for which the University of Glasgow awarded him a DSc in 1921. This book presents a masterful historical analysis of the form-function relationship from antiquity to the end of the nineteenth century, drawing almost exclusively on primary sources. The question that drives Russell's examination is simple: 'Is function the mechanical result of form, or is form merely the manifestation of function or activity? What is the essence of life—organization or activity?' (ibid., p. v). Russell identifies three general views playing out throughout history—the functional (or synthetic), the formal (or transcendental), and the materialistic (or disintegrative)—and he does not hide his predilection for the first, which is most closely associated with Aristotle and Georges Cuvier. Russell's subsequent works were more philosophical than historical, but he did eventually revisit the significance of the form-function dichotomy for the historical development of biological theory 20 years later (Russell, 1936b).

In appraising *Form and Function* in the historical context in which it appeared, some commentators (e.g., George Lauder in his introduction to the 1982 reissue of the book) have found it instructive to contrast it with D'Arcy Thompson's more famous *On Growth and Form* (1917), which appeared just a year later. Although the two authors had similar backgrounds—both were Scots, and both had dual training in classics and in the sciences—their respective biological viewpoints are in some respects strikingly different. While Thompson views organisms in formal terms as 'material and mechanical configuration[s]' amenable to physical and mathematical explanation (Thompson, 1917, p. 10), Russell views them functionally and holistically, 'as active, living, passionate beings like ourselves' that require an autonomous biological method to account for them (Russell, 1916a, p. 364).

What characterises Russell's engagement with the philosophical foundations of biology throughout his life is an intense preoccupation with the question of how to study and explain

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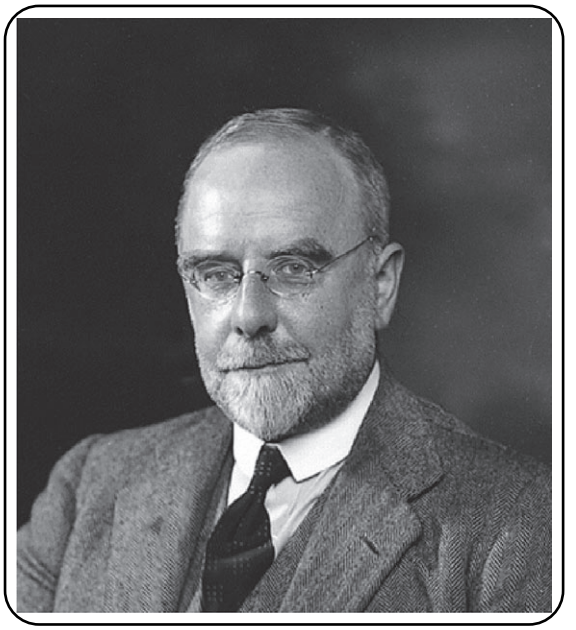

Figure 1 Edward Stuart Russell. Ramster et al. (2003)/Reproduced from Oxford University Press.

the organism in a way that does not lose sight of its most distinctive features. Already in 1911, Russell had argued that although the organism is clearly subject to the laws of physics and chemistry—life does not violate these laws, as vitalists like Hans Driesch had notoriously suggested—it is nevertheless inappropriate to presume that one can fully account for the integrated organization and activity of an organism in purely physicochemical terms. As Russell himself puts it,

> All vital activities can conceivably be analysed into a particular combination in space and time of processes each of which is explicable by physical and chemical laws; but it does not follow that the combination of these processes is itself explained by the laws which explain each single process. And it is just this particular combination which transmutes a complex of physical and chemical reactions into the activity of a living organism. (Russell, 1911, p. 330)

Biological phenomena, Russell maintains, call out for explanation in biological terms. The principles of biology cannot be completely reduced to those of physics and chemistry. He illustrates this with the migration of eels to the North Atlantic—a phenomenon that Russell himself had carefully studied—and notes that although one could in principle decompose the act of migration into an endless cascade of physicochemical reactions (such as those involved in muscle contraction, nervous conduction, the stimulation of peripheral sense organs, etc.), one would still not understand why the eel migrates (ibid., p. 336). More generally, Russell claims that one cannot comprehend the activity of any organism without referring to its developmental trajectory and to its evolutionary history.

Russell's concern with developing an interpretive framework that would permit the elaboration of a truly autonomous science of life—a genuine biology worthy of its name—is the central theme of his second book, *The Study of Living Things: Prolegomena to a Functional Biology* (1924a). After scrutinising the two traditional approaches to life, the mechanistic and the vitalistic, and finding both of them wanting (the former because it relies on the hopelessly inadequate conception of the organism as a machine, the latter because it posits a mysterious immaterial agency that endows the organism with its distinctive capacities), Russell considers two alternative points of view, which he calls the psychological and the biological. The psychological point of view stems from the pre-scientific, common-sense attitude that the layperson might display towards other living beings (not just other humans but also animals, plants, etc.), inasmuch as these are typically treated as 'individuals or subjects, each perceiving its own objective world, and reacting to this perceived world in such a way as to satisfy its own needs and desires' (ibid., p. 31). The biological method is more properly scientific, and it recognises the organism as a persistent, physiologically self-regulating and self-maintaining system. It requires that any biological phenomenon one may pick out for experimental study be interpreted as a manifestation of the unitary activity of the organism as a whole. This was the viewpoint developed by another Scot, the physiologist and philosopher of biology John Scott Haldane (father of the now better-known J. B. S. Haldane), in a number of publications (Haldane, 1913, 1917, 1919), which Russell duly cites. Ultimately, Russell advocated a synthesis of the psychological and biological views, which he believed presupposed one another. Organisms are perceptive subjects with a set of instinctive, irreducible impulses (which Russell terms 'hormé') *because* they are self-maintaining, persistent individuals. Russell called his approach 'psychobiology', and he developed it in the second half of *The Study of Living Things*, as well as in several essays (Russell, 1923a, b, 1924b).

In 1930 Russell published his most substantive philosophical work, titled *The Interpretation of Development and Heredity: A Study in Biological Method*. This book presents his fully developed biological philosophy, which Russell now called 'organismal biology', borrowing the term from William Emerson Ritter (1919). His focus is on the relation between development and heredity—one of the most formidable and pressing biological questions at that time, and one which other like-minded philosophers of biology were concurrently trying to tackle (e.g., Woodger, 1929, 1930; Bertalanffy, 1933). For Russell, to inquire into the nature of these phenomena is to come to grips with the fundamental problem of the relation of the parts to the whole. Accordingly, Russell asks himself:

> Is development essentially an activity of the organism as a whole, or can its full explanation be found by analysing the process into its constituent elements? Is heredity essentially the reappearance and realization of the functional potentialities of the whole, or are the separate characters of the organism transmitted piecemeal, being represented separately in material form in the germ? Are development and heredity functions of the organism as a whole, or functions of its cells, or of still smaller constituent units? In general, is the organism a real unity or individual, not

> completely reducible to its constituents, or is it a mere composite, built up as a hierarchy of independent units? (Russell, 1930, pp. 2–3)

As in *Form and Function*, Russell addresses these questions in conversation with the history of biological thought. He identifies two basic kinds of biological theory that reappear in different guises from antiquity to the present day (cf. Delage, 1895): unity theories (like those of Aristotle, Caspar Friedrich Wolff, Karl Ernst von Baer, and Edwin Conklin) and particulate theories (such as those of Hippocrates, Charles Bonnet, August Weismann, and Thomas Hunt Morgan). The former prioritise the whole over the parts, whereas the latter prioritise the parts over the whole. Russell's own organismal standpoint involves a particular version of the unity theory.

An interesting point of difference that Russell identifies in the theories he discusses is the degree to which they are willing to abstract away the organism as it presents itself in our experience for the purposes of its investigation. Most biologists will abstract the organism from the surroundings in which it is inextricably embedded and treat it as a distinct, autonomous unity. Some will go further and construe it as a complex mechanism so as to render it amenable to physicochemical explanation. And others will go as far as to resolve it analytically into a set of microscopic functional units or characters. Although abstraction and analysis are useful and to some extent indispensable in biology, Russell argues that they are often misused or abused (he also makes this point in Russell, 1933).

One of the core tenets of organismal biology is that in an organism—unlike in a machine—'there *are* no completely separable or independent parts; if we distinguish separate units or components it is at the cost of artificially simplifying our definition of them by abstracting from their continuing relations with the activity of the organism as a whole' (Russell, 1930, p. 146). To correct and caution against the excessive use of abstraction, Russell proposes two principles of biological method. The first is that '*The activity of the whole cannot be fully explained in terms of the activities of the parts isolated by analysis*' (ibid., p. 147). The second is that '*No part of any living unity and no single process of any complex organic activity can be fully understood in isolation from the structure and activities of the organism as a whole*' (ibid.).

Russell's endorsement of these two principles is what drives his detailed critique of modern particulate theories, which—interpreted in Mendelian terms—were becoming increasingly popular by 1930. Russell forcefully rejects both Weismann's (1893) germ-plasm theory and Morgan's (1926) chromosomal theory of the gene on similar grounds, claiming that both illegitimately posit the existence of a material substratum that determines the phenotypic characters of the whole organism. For Russell, it makes no sense to credit a part of the whole with the capacities of the whole. As he explains,

> If the activity of the organism as a whole is not completely reducible to the modes of action of its parts, then it follows that the modes of action of the whole, whether actual or potential, can be transmitted only by a whole, i.e. by the egg in its entirety, which at the very beginning of development *is* the new individual. Subordinate parts of the egg-organism can transmit only their own particular modes of action, and not the modes of action of the whole (Russell, 1930, p. 283).

The very idea of a hereditary substance magically endowed with all the powers of the whole organism is tantamount to postulating a materialised vital spirit—what Russell mischievously calls at one point a 'material entelechy' (Russell, 1930, p. 154). Following Wilhelm Johannsen (1923), and against Morgan and his followers, Russell contends that 'genes are purely hypothetical units—convenient (or inconvenient?) fictions invented to account for the very complex hereditary behaviour of mutant characters in *Drosophila*. As such they have a certain interpretative and heuristic value, provided that their purely conceptual and hypothetical character is clearly borne in mind' (Russell, 1930, p. 62).

More generally, Russell rejects the notion that heredity can be studied separately from development. Heredity is itself a feature of development, not a separate phenomenon. Positing imaginary entities stored in the cell nuclei does nothing to advance our understanding of cell differentiation or of morphogenesis. Chromosomes are of course instrumental in the complex cascade of biochemical reactions that set the developmental process in motion, but these processes always take place in the context of an already organized and integrated whole (the zygote), to which they are necessarily subservient; they cannot by themselves be regarded as causally responsible for development.

The last book Russell published in his lifetime was *The Directiveness of Organic Activities* (1945). It provides an extended defence of what Russell considers to be the most fundamental feature of life, namely its intrinsically purposive or teleological character. However, to ward off accusations of vitalism or mysticism, and to signal that this feature is a perfectly legitimate object of scientific inquiry, Russell eschews philosophically loaded concepts like 'teleology' and 'purposiveness' in favour of more neutral-sounding terms like 'directiveness' and 'creativeness'. What makes organisms different from non-living things (like machines), Russell claims, is that their activities—and those of their constituent parts—are directed towards end-states or goals that ultimately contribute to the biological ends of self-maintenance, development, or reproduction. The active pursuit of these three ends in one continuous life cycle is what gives the organism its coherence as a functional and organizational whole.

Although Russell's agenda in this book is unmistakably philosophical, his approach to the subject is strictly empirical. Most of the chapters consist of systematic descriptions of actual examples of what he means by 'directiveness' and 'creativeness', drawing on an impressively wide range of cellular, developmental, physiological, and behavioural phenomena. In presenting and discussing this wealth of empirical material, Russell deliberately avoids getting entangled in philosophical questions, declaring that 'I make no hypothesis as to the nature or philosophical ground of directiveness; I accept it as a fact' (ibid., p. 80). Only in the last chapter of the book, titled 'The Concept of Organism', does he venture into philosophical waters and attempts to tease out the implications of his view. Chief among them is his contention that

'human directiveness or purposiveness in thought and action are a specialised development of the directiveness and creativeness inherent in life' (ibid., 178). By interpreting psychological activity as a form of vital activity (both of which are directive), Russell suggests that we might be able to overcome the classic Cartesian dichotomy between mind and matter.

In the last years of his life, Russell continued to write about the purposiveness of organisms. He wrote a paper on this topic for a philosophical audience (Russell, 1950), and another with historians in mind on the biological ideas that Arthur Schopenhauer set forth in his 1836 treatise *On the Will in Nature* (Russell, 1953). Russell died in 1954 aged 67. The obituary published in *Journal du Conseil*—which Russell had edited for 15 years—remarked that '[t]o those who knew him well, [Russell's death at the early age of 67] could not come as a great surprise, because his health was never good, and the key to his life's work lay in this, that by force of intellect and character, he was effective and permanently constructive within the strict limits set by a weak heart' (Graham, 1954, p. 135).

Russell's final work, *The Diversity of Animals: An Evolutionary Study* (1962), was published posthumously by the editors of the Dutch theoretical biology journal *Acta Biotheoretica* in their associated monograph series *Bibliotheca Biotheoretica*. Russell had maintained a lifelong interest in evolutionary theory, as some of his earliest publications show (Russell, 1909, 1916b), but it was only in this final book, which sadly remained unfinished at the time of his death, that he fully turned his attention to evolution. Structurally and stylistically, the book is somewhat similar to *The Directiveness of Organic Activities* in that although much of it consists of detailed and rather technical discussions of the diverse morphological features of different animal species—with a particular emphasis on decapod crustaceans (e.g., crabs, lobsters, crayfish, shrimp, etc.)—Russell's aim is much more general and theoretical. His objective is to account for the origin of the diversity of animal forms, and he does so by putting forward a non-Darwinian, orthogenetic theory of evolution. According to this theory, major evolutionary changes are directed by the internal tendencies that organisms display during the early stages of their development. An obvious implication is that, for Russell, an understanding of development is essential for explaining evolution—something that is generally recognised by biologists today.

It should be clear from this brief discussion of Russell's rich oeuvre that not all his works have aged equally well. *Form and Function* is reasonably well known today among evolutionary developmental biologists owing in large part to George Lauder, who convinced Chicago University Press to reissue the book in 1982 and for which he wrote an extended introduction. Professional historians of biology have also praised the book. William Coleman (1977, p. 168) wrote that '[n]o work has replaced [it] as a comprehensive […] account of nineteenth-century views on the nature and formation of the organism. Russell's book largely defined its field and by so doing made intelligible a vast amount of otherwise confusing and seemingly unrelated biological study'. More recently, Ruse (2003, p. 225) has noted that Russell is 'still the best historian of the form/function relationship'. On the other hand, some of Russell's philosophical ideas and positions, such as his concept of hormé and the psychobiological standpoint he defended in the 1920s, are of more questionable contemporary relevance. This is also the case for Russell's orthogenetic theory of evolution put forward in *The Diversity of Animals*, which has been—perhaps understandably—almost completely forgotten.

What is most striking when considering Russell's legacy is the changing fortune of *The Interpretation of Development and Heredity*, as Stephen Talbott (2009) and Maurizio Esposito (2013) have recently observed. For a long time, this book was derided—if not altogether ignored—for its obstinate refusal to accept the chromosome theory of the gene, which appeared to have been conclusively confirmed by the mid-twentieth century. Nils Roll-Hansen (1984) subjected the book to a scathing critique, blaming Russell for having dogmatically 'opposed mechanistic biology with a priori arguments' (ibid., p. 427) and judging his entire anti-reductionistic philosophy of biology to have been a scientific failure. In the context of the 1980s—a time when the gene was at the height of its influence upon the biological imagination (one need only remember the 'selfish genes' of Richard Dawkins or the 'master control genes' of Walter Gehring)—one might have been forgiven for assuming that the issue had been settled for good. In the present context, however, things look remarkably different.

A geneticist today, upon hearing the view that genes are 'pure abstractions' (Russell, 1930, p. 155) that do not correspond to neatly delineated material parts of the cell, might assume that this claim had been made by a colleague. The notion of a clearly defined, causally efficacious gene that can be construed independently of everything else that is going on in the cell has been questioned so many times in recent decades that some contemporary commentators have gone as far as to suggest that it would be preferable if the gene concept was abandoned altogether. This was Evelyn Fox Keller's famous diagnosis in *The Century of the Gene* (2000, p. 69), where she asserted that recent empirical findings 'have brought the concept of the gene to the verge of collapse'.

From today's perspective, then, Russell does not seem to have been so utterly misguided when he predicted that a time would come in biology when 'the gene will cease to be regarded as a self-existent particulate unity and will be merged in the general physiological activity' of the whole cell (Russell, 1930, p. 157). A growing number of molecular biologists no longer think it is possible to realistically define a gene as a specific segment of deoxyribonucleic acid (DNA) with a fixed identity independently of the rest of the cellular context. The term 'gene' is instead increasingly regarded as a convenient way of referring to a complex constellation of cellular events. Again, this is a sentiment that one finds prophetically expressed in Russell's book: '*The gene is a word*, which enables a complicated happening to be briefly denominated' (ibid., p. 67).

Finally, books like *The Study of Living Things* and *The Directiveness of Organic Activities*, which for decades faded completely out of view, appear to be acquiring a new relevance as well in light of the renewed interest among biologists and philosophers today in the nature of organismic agency. Only time will tell if Russell's organismal views will also eventually be taken to have been vindicated.

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