

# In What Sense Does ‘Nothing Make Sense Except in the Light of Evolution’?

Paul Edmund Griffiths

Received: 29 June 2008 / Accepted: 25 August 2008 / Published online: 6 September 2008  
© Springer Science+Business Media B.V. 2008

**Abstract** Dobzhansky argued that biology only makes sense if life on earth has a shared history. But his dictum is often reinterpreted to mean that biology only makes sense in the light of adaptation. Some philosophers of science have argued in this spirit that all work in ‘proximal’ biosciences such as anatomy, physiology and molecular biology must be framed, at least implicitly, by the selection histories of the organisms under study. Others have denied this and have proposed non-evolutionary ways in which biologists can frame these investigations. This paper argues that an evolutionary perspective is indeed necessary, but that it must be a forward-looking perspective informed by a general understanding of the evolutionary process, not a backward-looking perspective informed by the specific evolutionary history of the species being studied. Interestingly, it turns out that there are aspects of proximal biology that even a creationist cannot study except in the light of a theory of their effect on future evolution.

**Keywords** Teleology · Function · Dobzhansky · Millikan

## 1 Dobzhansky’s Dictum

Classic scientific articles are often more cited than read. ‘Nothing in biology makes sense except in the light of evolution’ by the Ukrainian-American geneticist Theodosius Dobzhansky (1973) is no exception. It argues that the observed diversity of life and its distribution on the earth’s surface make no sense when viewed as the result of the special creation of each species by God. These observations make good sense, however, when viewed as the result of evolution. They are the kinds of patterns we would expect to see if life on earth had evolved. To a large extent

---

P. E. Griffiths (✉)  
University of Sydney, Sydney, Australia  
e-mail: paul.griffiths@usyd.edu.au

Dobzhansky drew on the same sources of evidence as Darwin: comparative anatomy, embryology, and biogeography. But writing in the 1970s he could supplement this evidence with early examples of what we would today call comparative genomics and comparative proteomics. Like the distribution of characters in anatomy and embryology, the observed distribution of molecular characters makes sense only if the genomes that exist today have a shared ancestry. Dobzhansky himself, an Orthodox Christian as well as a leading geneticist, argued that God used evolution to produce the diversity of life.

So far Dobzhansky himself, biology only makes sense in the light of evolution because it only makes sense if life on earth has a shared history. This shared history is sometimes called the ‘fact of evolution’ in contrast to the ‘mechanism of evolution’. Dobzhansky had no doubt that natural selection is the basic mechanism of evolution, but he accepted that there was room for dispute about how natural selection operates and how it interacts with other proposed mechanisms such as drift. ‘Evolution as a process that has always gone on in the history of the earth can be doubted only by those who are ignorant of the evidence or are resistant to evidence, owing to emotional blocks or to plain bigotry. By contrast, the mechanisms that bring evolution about certainly need study and clarification.’ (Dobzhansky 1973, p. 129. For more on the original intention and context of Dobzhansky’s article, see Burian 2005, Ch. 6).

**Fig. 1** Dobzhansky in 1955 near the Cristo Redentor de los Andes monument on the Chile/Argentina border. Photo courtesy of Charles Birch



Today, however, Dobzhansky’s dictum is often understood in a different sense. It is taken to mean that the structure of living organisms only makes sense when viewed as a set of evolutionary adaptations to specific selection pressures. Nothing in biology makes sense except in the light of *adaptation*. For example, the dictum is cited in support of the view that psychology will make better progress once it learns to see the human mind as a set of adaptations to the human ‘environment of evolutionary adaptedness’ (e.g. Gintis 2007). The view that nothing makes sense except in the light of adaptation has also been endorsed by some philosophers of science, as I discuss in Sects. 2 and 3 below. Philosopher Alexander Rosenberg has argued that the structure of the genome only makes sense when viewed as a set of adaptations and that individual genes are, or at least should be, defined by the purposes for which they are adapted (Rosenberg 2001). In these discussions it is clear that what is meant by ‘makes sense’ is not only that biological phenomena are as we would expect them to be if they had been produced by these selection histories, but also that classifying biological parts and processes as the products of particular selection histories is a productive way to frame investigations into the details of their form and function.

These recent ideas are a long way from what Dobzhansky meant when he formulated his famous dictum. His article makes frequent reference to the process of adaptation, but it does not use the fact that organisms are well adapted to argue for the reality of evolution. It was obvious to Dobzhansky, as it was to Darwin, that evolution by natural selection and special creation *both* predict that organisms will be well adapted. But only evolution predicts the patterns seen in comparative biology and in biogeography. For example, Dobzhansky pointed out that the Hawaiian islands have a diversity of *Drosophila* species unmatched anywhere else on earth. This is the sort of pattern that evolution leads us to expect, since the Hawaiian islands are geologically young and geographically isolated. Whichever species first colonised them would have an opportunity to fill a range of unoccupied ecological niches. On the hypothesis of special creation, however, the extraordinary diversity of the Hawaiian relatives of the fruit fly can only be explained as a piece of divine whimsy.

My focus in this article is on philosophical arguments in favour of the modern reinterpretation of Dobzhansky’s dictum, according to which nothing makes sense except in the light of *adaptation* (Millikan 2002; Neander 2002; Rosenberg 2001, 2006). There are two main arguments to confront, both of which are most clearly stated by Ruth Millikan. The first is that evolutionary history distinguishes an organism’s biological functioning from processes that are not part of its biological functioning. Kangaroos eat grass and also get caught in bushfires, but kangaroo physiology only studies the former of these two processes. It is the selective history of the kangaroo that makes it correct to study the physiology of the kangaroo’s digestive system, but not the ‘physiology’ of the kangaroo’s ‘combustion system’. The second argument is that the selection history of an organism defines the parts and processes into which that organism can be divided. This particular part of the kangaroo is a colon, not a liver, and that parasitic worm is not part of the kangaroo at all. These distinctions, it is alleged, only make sense in terms of the selective history of the kangaroo. Taken together these arguments suggest that even the most apparently straightforward, descriptive work in biology implicitly makes claims about the adaptive purpose of the parts and processes that are described. However,

despite its superficial appeal, the view that ‘nothing in biology makes sense except in the light of adaptation’ leads to paradox. If it were true, then we could not do biology, as I show in Sect. 4.

In the past few years a number of other philosophers of science have questioned the idea that nothing in biology makes sense except in the light of evolution, whether in Dobzhansky’s original sense of shared history or in the revised sense of a history of adaptation (Weber 2005; Wouters 2005a, b, 2007). They have pointed out that much successful research in fields such as physiology and molecular biology is conducted by scientists who have minimal information about the evolution of the parts and processes they study, that those scientists often evince little interest in finding out the details of their evolution, and that the acquiring knowledge of those details would be very difficult. They make a powerful *prima facie* case that these areas of biology make sense without the light of evolution, as I describe in Sect. 5. In Sects. 6 and 7, however, I will show that this second group of philosophers are also mistaken and that we do need an evolutionary perspective in order to make sense of physiology, molecular biology and the like. Ruth Millikan and others are correct in their contention that an evolutionary perspective is needed to identify which activities count as ‘biological functioning’. But the evolutionary perspective which plays this role does not view organisms as things that have evolved, but as things that are evolving. It is a forward-looking perspective informed by a general understanding of the evolutionary process, not a backward-looking perspective informed by the specific evolutionary history of the species being studied. So one important part of this paper will be to distinguish these two very different senses in which one can speak of an ‘evolutionary perspective’.

## 2 Defining Biological Function

There are two, key senses of function in the biological sciences (Godfrey-Smith 1993; Griffiths 1992, 1993). One is selected function, also known as ‘selected effect’, ‘etiological’ or ‘proper’ function (Millikan 1984; Neander 1991a). The other is causal function, also known as ‘causal role’ or ‘Cummins’ function (Cummins 1975, see also Wimsatt 1972). The difference between these two senses can be made clear by an example:

- Selected function: a sequence of nucleotides TATAAA has the selected function of binding transcription factors if that sequence evolved by natural selection because it had the effect of binding transcription factors in ancestral organisms.
- Causal function: a sequence of nucleotides TATAAA has the causal function of binding transcription factors if that sequence has the effect of binding transcription factors in the organism in which it occurs.

The distinction between these two notions of function is closely related to the conventional neo-Darwinian distinction between *adaptations*, which have evolved by natural selection, and *adaptive traits*, which increase the fitness of organisms that possess them relative to other types. Every adaptation was once an adaptive trait, but not all adaptations are still adaptive. Conversely, not every adaptive trait has the

selective history required to make it an adaptation. A trait is an *adaptation* if it has some selected function(s). A trait is *adaptive* if it has causal functions which contribute to the overall fitness of the organism.

There has long been a consensus that only selected function is genuinely teleological or ‘teleonomic’ (Pittendrigh 1958; Brandon 1981). Hence only selected function can be used to distinguish a trait’s functioning from the same trait malfunctioning or having biologically irrelevant side-effects (Millikan 1984; Neander 1991b; Papineau 1987). A standard example is supposed to make this clear: the sounds made by the human heart, although very useful to doctors, are a mere side effect. Making a noise that can be detected through a stethoscope is not one of the functions of the human heart. The philosophical consensus is that this is true because the sounds made by the heart did not increase the fitness of our ancestors relative to their evolutionary rivals. But I have come to doubt that this is the only way in which biologists distinguish between function, malfunction and side effect (see particularly Griffiths 2006). Other recent authors who have departed from this longstanding consensus include Paul Sheldon Davies and Tim Lewens (Davies 2001; Lewens 2004). The older literature on functional analysis also recognised that there may be reasons other than their evolutionary role for singling out some functions as those in terms of which performance should be evaluated (Cummins 1975, 1983; Wimsatt 1972).

There are clearly some contexts in which the function/malfunction/effect distinction is drawn by looking at adaptation. These are contexts in which scientists are focusing on evolutionary questions. Suppose for example, that a behavioural ecologist asks whether it is the function of individual variation in birdsong to allow individual recognition by conspecifics, or whether this is only a side effect. Perhaps individual recognition is the unavoidable consequence of conveying information about mate quality. It is plausible to interpret this question as asking about the selection pressures that shaped birdsong. But this interpretation is often implausible when applied to questions in ‘proximal’ (Mayr 1961) or ‘experimental’ (Weber 2005) areas of biology—disciplines such as anatomy, physiology, developmental and molecular biology. In these contexts I do not believe that attempts to identify the function of parts and processes are typically attempts to identify the purposes for which those parts and processes are adaptations. This is not to say that the functions identified by these sciences do not in many cases coincide with selected functions of the relevant parts. The point is that ‘proximal’ biologists do not need to take a stand on this, historical question in order to correctly identify function. The identification of function in these biosciences seems to be a straightforward experimental matter. Ascriptions of function are confidently made by biologists who take organisms apart and examine their workings but do not test hypotheses about their evolution. Identifying the selection pressures that drove the evolution of these parts and processes would be far more difficult and would require additional forms of evidence that these scientists simply do not collect (Amundson and Lauder 1994; Pigliucci and Kaplan 2006). This suggests that they are not ascribing selected function but something closer to causal function.

The view that I will defend later in this paper is that these function ascriptions correspond to a special set of causal functions—roughly, those that contribute to the

causal capacities of the organism that are relevant to understanding its evolutionary fate. This is a ‘forward-looking’, evolutionary sense of function as opposed to the backwards-looking evolutionary sense of selected function. Forward-looking evolutionary analyses of function ascriptions in biology have been proposed before (Bigelow and Pargetter 1987; Canfield 1964), but the view that such a sense of ‘function’ plays a significant role in biology has never been widely accepted.

### 3 Defining Biological Functioning

The view that the parts and processes of organisms are defined by their selected functions was made popular by the writings of Millikan and Karen Neander (see especially Millikan 2002; Neander 2002), although it has also been strongly advocated by Rosenberg (2001, 2006). Millikan offers a very general argument for supposing that biological characters *must* be defined by selected function. She argues that a purely descriptive biology, unaided by evolutionary teleology, has no principled way to determine what counts as the system in need of analysis. Biologists need to identify whether something is part of an organism’s biological functioning, as opposed to an irrelevant causal processes like the process a kangaroo undergoes when it is burnt in a bushfire. Biologists also need to distinguish normal traits from pathologies, and to delimit the boundaries of a single organism, so as, for example, not to confound the kangaroo and its fleas. However,

Living chunks of matter do not come, just as such, with instructions about what are allowable conditions of operation and what is to count as allowable input. Similarly, they do not come with instructions telling [*what is*] damage, breakdowns or wear-downs. Nor do they come with instructions about which processes...are to count as occurring within and which are irrelevant or accidental to the system. (Millikan 2002, p. 121)

Millikan’s point is that it is not simply given which parts of the physical world, and which properties of those parts, form the subject matter of biology. The three problems she identifies are all aspects of defining which parts and processes constitute the biological functioning of an organism.

These are not trivial problems. For over a century after sperm were first observed in 1678 the hypothesis that they were part of the mechanism of generation was confronted by the rival hypotheses that they were parasites or that they were the results of decay like the microorganisms observed in many other liquids derived from living matter (Gasking 1967). Some investigators who accepted that sperm were part of the mechanism of generation hypothesised that their function was to agitate the seminal fluid with their flagella. Even today it is debated whether the some of the different sperm morphologies seen in a single ejaculate have specialised functions or whether they are pathological (Moore et al. 1999). So although it is easy to forget about these problems in areas of biology where they have been solved, the problems are real. The question is how biologists solve them.

According to Millikan, the problem of defining biological functioning is solved by studying only those features of an organism which represent evolutionary design,

and by classifying the parts of the organism in terms of the purposes for which they were designed—their selected functions. For example, a riboswitch is a region of untranslated mRNA that regulates expression of the gene from which it is transcribed by directly binding a metabolite. One of the first riboswitches was identified in the leader sequence of the *btuB* RNA in *E. coli* (Nahvi et al. 2002). It was already known that RNA can bind these sorts of small metabolites, and that this can affect RNA folding, but it was not known that living organisms made use of this fact to regulate the expression of their own genes. The significance of Nahvi et al. findings and other similar findings around the same time was that a process that was known to be biochemically possible was shown to be part of the biological functioning of real organisms. On Millikan’s account, Nahvi et al. were correct and this process is part of the biological functioning of *E. coli* only if it has the selected function of controlling gene expression, that is to say, if the nucleic acid sequences involved were designed by natural selection to control gene expression in the way that they do. However, as some critics have pointed out, molecular and cell biologists show little concern to provide evidence for such evolutionary assumptions when determining the function of molecular parts and processes (Weber 2005, pp. 35–41; Wouters 2005b). Nahvi et al. no doubt assumed that the *btuB* riboswitch was the product of natural selection, but they do not explicitly discuss this. In fact, the discussion of evolution in their paper is confined to noting that key elements of the riboswitch are evolutionarily conserved and hence that metabolite sensing by RNAs may have evolved early in the history of life. Critics of the selected function account have proposed alternative ways to distinguish biological functioning from biologically irrelevant processes which I discuss in Sect. 5. The point of these alternative analyses is not to deny that things like the *btuB* riboswitch are adaptations, but to show that experimental biologists do not need to establish that they are adaptations, let alone the details of their adaptive history, before they can determine their function.

Millikan allows one important class of exceptions to the rule that only parts and processes have been produced by natural selection are part of an organism’s biological functioning. She notes that activities that have been produced by natural selection often rely upon parts and processes whose evolution has been entirely independent of selection for those activities. For example, the ability to blush depends on the redness of blood, but the selective advantages of blushing, whatever they may be, do not explain why human beings have red blood. The contributions of such adventitiously recruited parts to activities that have been produced by natural selection are part of biological functioning (Millikan 2002). Millikan suggests that the well-known term ‘exaptation’ is best defined as this use of adventitiously recruited pre-existing parts to support new selected functions, a somewhat narrower definition than the usage common in biology (e.g. Gould and Vrba 1982).

A perspective apparently similar to Millikan’s was adopted by the founders of the modern, Darwinian study of behaviour Konrad Lorenz and Niko Tinbergen. With his sights firmly on the behaviourist tradition, Lorenz sniped that “in many branches of the psychological and behavioural sciences it is today quite usual to devise, out of hand, some sort of experimental procedure, apply it to a highly complicated system about which next to nothing is known, and then record the results” (Lorenz 1966,

p. 274). To use one of Millikan's metaphors, this is like studying washing machines by putting them in outer space, or deep in the ocean, and recording the results of these interventions. Lorenz and Tinbergen insisted that students of behaviour must examine how animals make a living in their natural environments before subjecting them to controlled experimentation. The proper object of washing machine research is clothes-washing, and the proper object of animal behaviour research is how animals accomplish the tasks that allow them to survive and reproduce in their natural environments. However, while I agree that an evolutionary perspective is essential to correctly identify what counts as biological functioning, I will argue below that it must be a forward-looking and not a backward-looking evolutionary perspective.

#### 4 A Paradox for Millikan

Millikan has correctly pointed out that in order to study the biological functioning of an organism, biologists must identify where one organism ends and another begins, must distinguish the functioning of that organism from irrelevant causal processes in which the organism is caught up, and must identify and exclude pathological features of the organism. She suggests that biologists determine whether something is part of an organism's biological functioning, and thus solve these problems, by determining that it has a selected function (or has been exapted to support a selected function). But this suggestion generates a paradox, because the first step in determining whether something has a selected function is to analyse the contribution it made to biological functioning in the past. To show that oddly-shaped sperm have the selected function of interfering with the sperm of rival males, it is necessary to show that these sperm increased the fitness of ancestral males that produced them by interfering with the sperm of rival males. But either we can establish this without knowing the selected function of the sperm of those ancestral males, in which case we could do the same for living males, or we have to know their selected function in those ancestors, which means looking at still earlier ancestors to discover this and so on ad infinitum. This argument can be laid out a little more formally as follows:

1. Ascriptions of selected function are generated by causal analysis of the capacities of ancestral organisms to survive and reproduce in ancestral environments.
2. Hence, if we cannot identify which capacities of ancestral organisms to subject to causal analysis without knowing what the parts of those organism were selected for in *their* ancestors, then we face a vicious regress.
3. Therefore, a purely causal analysis of how the parts of ancestors were *adaptive* must be possible without knowing what those parts were *adaptations for*.<sup>1</sup>
4. If this is possible for ancestors, it is possible for living organisms.

<sup>1</sup> I am using 'adaptive' and 'adaptation' in the conventional, neo-Darwinian sense outlined in Sect. 2 above. A trait is adaptive if a Cummins-style (1975) functional analysis of an organism's fitness assigns a causal function to that trait. Something is an adaptation if it has a 'modern history' selective function sensu Godfrey-Smith (1994, see also Griffiths 1992, 1993).



Let me be clear what I am *not* saying. I am not denying that biologists can establish the selected function of parts and processes. I am merely denying that they can establish these selected functions as a first step *before* describing the causal functions of those parts and processes. Moreover, I am not denying that proximal biology is in some sense illuminated by our understanding of evolution. In fact, I will explain in just which sense this is true in Sect. 6. My point is that if biologists really needed to make progress in understanding why something evolved before they could begin to study what it does, then they could never get started. Biologists must have some way of doing proximal biology without information about the selected function of the parts and processes which they are studying. But Millikan has argued cogently that biologists cannot simply look at complex living systems with a naïve eye and automatically discern what counts as biological functioning. So it is time to consider the philosophers who have suggested other, non-evolutionary ways in which to define biological functioning.

## 5 Can Biology Do Without An Evolutionary Perspective?

The leading advocate of the view that some areas of biology can do without an evolutionary perspective is Arno Wouters (1995, 2003, 2005a, b):

Functional biology without evolution is incomplete in the sense that it ignores many important questions about life, but not in the sense that no aspect of life can be understood without invoking evolution (Wouters 2005a, p. 55).

In traditional biological usage ‘functional biology’ is the study of the mechanisms by which organisms do what they do, in contrast to evolutionary biology, which explores why organisms possess these mechanisms (Bock and von Wahlert 1965). The functional/evolutionary distinction is roughly equivalent to Ernst Mayr’s distinction between proximal and ultimate biology (Mayr 1961). The biological usage can be a little confusing in the context of philosophical discussions which links the term ‘function’ so closely to teleological explanation, and hence to the evolutionary or ‘ultimate’ side of these same dichotomies.

According to Wouters, biologists do not pick out the subject matter of functional biology in terms of evolution, and especially not natural selection. He defines something similar to what I have called ‘causal function’ which he calls ‘biological role’: “the manner in which that item/activity contributes to the activity of a complex system”. He contrasts biological role to what he calls ‘biological advantage’—“the way in which that trait influences the life chances of an organism as compared to other traits that might replace it” (Wouters 2005a, pp. 41–42). Whilst biological role seems to be the same thing as causal function, biological advantage is nothing like selected function. Selected function is an historical notion, defined in terms of the actual selection pressures that determined the success or failure of the actual ancestors of the organisms whose parts have selected functions. Biological advantage is an ecological, rather than an historical notion. It can be studied in living organisms without making any assumptions about their history, although it does require assumptions about the environment in which they live and about

biologically plausible alternatives that either already exist or might easily evolve in future. In effect, the study of biological advantage is the study of what Tinbergen called ‘survival value’: “whether any effect of the observed process contributes to survival if so how survival is promoted and whether it is promoted better by the observed process than by slightly different processes.” (Tinbergen 1963, p. 418) In contemporary biology these sorts of questions are often tackled using optimality analysis and evolutionary game theory.<sup>2</sup> I will have more to say about these forward-looking evolutionary questions in the next section.

Wouters’ claim that functional biology studies biological role (causal function) as well as biological advantage raises an obvious question. Organisms have many complex capacities, most of which are biologically irrelevant as Millikan and other have pointed out. The parts and processes that make up organisms can be assigned causal function relative to any of these overall capacities. Most obviously, the parts of the body can be assigned causal functions relative to each of the disease processes the body is able to undergo. For example, an oncologist may seek to unravel the functions of the p53 protein in the genesis of tumours. Organisms have many equally complex capacities that are less obvious. Jared Diamond was the first to analyse the capacities of different plants and animals to facilitate the rise of dominant world-powers from their bioregions in virtue of their nutritional content, amenability to domestication, and so forth (Diamond 1997). Diamond’s work may be a contribution to ecology, very broadly construed, but these capacities are not part of the usual subject matter of functional biology. The capacities identified by pathologists and by Diamond’s work are, of course, interesting in their own right. If we let our imaginations run riot we can identify any number of more frivolous complex capacities which are none the less real for being frivolous. So a conception of biological role which can underpin a plausible definition of the subject matter of functional biology must pick a specific and appropriate overall capacity of the organism. The contributions of parts and processes to this capacity will make up the specifically *biological* role of those parts and processes. In his earlier papers Wouters conceived this overall capacity as ‘viability’—the ability to stay alive. Functional biology constructs ‘viability explanations’ (Wouters 1995). In more recent papers Wouters has developed a slightly different conception of explanation in functional biology which he calls ‘design explanation’ (Wouters 2007). Design explanations are specifically *contrastive* explanations of organisms’ ability to stay alive. The actual traits of organisms are shown to allow them to maintain themselves as living systems whilst other, real or hypothetical alternative structures would not do so or would do so less effectively. Wouters has developed a number of detailed case-studies of explanation in physiology that appear to work in just the contrastive manner he describes, and which pay little or no attention to the specifics of selection

---

<sup>2</sup> These methods are frequently used to establish what traits are adaptations for (their selected function) as well as whether and how traits are currently adaptive. The account of evolutionary explanation which I advocate in Sect. 7 below would imply that when this occurs these methods are either 1. Applied to hypothesised ancestral organisms in hypothesised ancestral environments, or, 2. Applied to current organisms on the assumption that the selective advantage they now confer is one they also conferred in the past. Criticisms of both these uses of optimality analysis can be found in the literature on ‘adaptationism’ (Dupré 1987; Gould and Lewontin 1978; Orzack and Sober 2001).

history. These explanations contrast the actual trait with hypothetical traits which could never have been evolutionary competitors (because they simply do not work) as well as with traits which might have been present in the evolutionary past.

Other non-evolutionary accounts of the subject matter of functional biology have strong affinities to that of Wouters. The philosopher and neurobiologist Gerhard Schlosser has argued that function ascriptions in biology identify the causal contributions of parts and processes to an overall capacity for ‘self-re-production’. A self-re-producing system is one that can “pass through cyclic sequences of states and thereby keep stable in the long run, despite changing continuously” (Schlosser 1998, p. 312). A similar account was proposed by Wayne Christensen (1996) and another has been defended in considerable detail by Peter McLaughlin (2001). A related approach has been defended by Craig Delancey (2006), and physiologist Benoni Edin has recently argued that physiologists assign functions to parts and processes when they make a certain distinctive sort of contribution to solving a problem of ‘active self-maintenance’ (Edin 2008). Whilst these authors concentrate on the analysis of function locutions, Marcel Weber has developed a broader account of explanation in what he calls ‘experimental biology’, a category encompassing much the same group of biosciences as Wouter’s functional biology. Weber’s vision of an analytic hierarchy of causal role functions is in the tradition of Robert Cummins classic account of functional explanation (1975; see also 1983). In the recent philosophical literature the concern with naturalising the function/malfunction distinction has overshadowed the analysis of less strongly teleological function language. Work from the 1970s, such as Cummin’s and that of William Wimsatt (e.g. 1972, 2007) remains amongst the most insightful on the subject. In Weber’s version of causal-functional analysis role functions are ascribed relative to some larger role function of a containing system, with this hierarchy of roles terminating in ‘some ultimate system capacity or system goal’ (Weber 2005, p. 39). He suggests that this ultimate system capacity may be McLaughlin’s ‘self-reproducibility’, which is the capacity of the system to maintain its form over time. This ‘self-reproduction’ must be distinguished from reproduction—generating new individuals with the same form. Weber argues that an account of how experimental biology defines its subject matter should be applicable to sterile individuals as well as to individuals who can reproduce themselves. Sterile individuals ‘self-reproduce’ through their lives in McLaughlin’s sense, but cannot reproduce.<sup>3</sup>

The idea that proximal biology can do without an evolutionary perspective has seemed compelling to several philosophers and biologist, each of whom have focused closely on the actual practice of some area of proximal biology. However, I will show in the next section that there are a number of cases in which the criteria they have proposed cannot distinguish biological functioning from irrelevant causal processes. The plausibility of non-evolutionary analyses, I will argue, comes from the fact that they give the same answers as an evolutionary analysis on the specific topics with which sciences such as anatomy and physiology have traditionally been

<sup>3</sup> On the view I advocate below sterile individuals could be dealt with by analysing the causal contribution of parts and processes to their inclusive fitness, which may be the correct approach for e.g. sterile castes in social insects, or by regarding them as pathological, which may be the correct approach for sterile hybrids e.g. mules.

concerned. But we have already seen that the standard evolutionary analysis leads to a paradox. In Sect. 7, therefore, I offer an alternative evolutionary analysis which avoids the paradox.

## 6 Why We Cannot Do Without An Evolutionary Perspective

Non-evolutionary accounts of biological functioning draw the boundary between biological functioning and other, irrelevant causal processes in which organisms are participants in the wrong place. They exclude activities which no-one can seriously doubt are examples of biological functioning. This happens because ‘viability’, ‘self-reproduction’ and the rest are only one component of a more encompassing ability which involves activities whose focus is not on the maintenance of the physiological individual. For example, the genetic and developmental mechanisms that underpin the failure of the mouthparts of mayflies to develop fully after metamorphosis to the adult reproductive stage make no sense when analysed for their contribution to the individual’s ability to maintain its form (‘self reproduction’). They make perfect sense as a contribution to reproduction. In several small Australian *Dasyurid* species such as *Antechinus Stuartii* a frenzied mating season is followed by a short period during which the male’s sexual organs regress and their immune system collapses. Then all the males in the population die. The mechanisms that underpin this ‘big bang mating’ behaviour (Diamond 1982) obviously do not contribute to the capacity of individual males to maintain their form. But they do contribute to the life-history strategy by which these males maximize their contributions to future generations. Biologists who study these mechanisms are not making a mistake like that of studying the ‘combustion system’ of kangaroos that get caught in bushfires. The self-immolation of the male *Antechinus* is clearly part of its biological functioning.

Such examples show clearly that biological functioning must be understood in terms of reproduction, not only self-reproduction. To the extent that the non-evolutionary accounts listed in the last section ignore reproduction, they are clearly inadequate. However, Weber’s explicit disavowal of reproduction is not representative of the literature as a whole, nor does it seem like a central feature of Weber’s account of causal-functional explanation. These authors are primarily concerned to distinguish their views from views which advocate the backwards-looking evolutionary definition of biological functioning as selected functioning. This leads them to downplay the functional analysis of reproductive fitness, even when this was not their intention. Wouters, for example, always intended ‘design explanation’ to encompass the design of reproductive mechanisms (personal communication). To the extent that the neglect of reproductive fitness by these authors is merely a matter of emphasis and choice of examples, the view that I present in this paper can be seen as a friendly amendment.

But although the reintroduction of a new, forward-looking evolutionary perspective may be compatible with the central tenets of the ‘non-evolutionary’ accounts, it leads to a very different vision of what functional biology is trying to explain. Taking an evolutionary perspective involves much more than merely

adding ‘reproduce’ to ‘survive and reproduce’. The phrase ‘survive and reproduce’ encompasses everything an organism does which has an effect on evolutionary dynamics. Because of this, advances in evolutionary theory can imply substantial revisions in what we take to be biological functioning and what we take to be irrelevant causal processes in which organisms are caught up. For example, the Trivers-Willard hypothesis suggests that females can increase their fitness by producing different sex ratios in response to seasonal fluctuations in resource abundance. When resources are abundant, females should invest more resources in the sex with the higher variance in offspring number, typically males. This insight led New Zealand conservation biologists to realize that the male-skewed sex ratio that was hampering their efforts to save the Kakapo (*Strigops habroptilus*, a large flightless parrot) was not merely a run of bad luck, but a response to the supplementary feeding program that was part of the conservation effort (Clout et al. 2002). By enriching the birds’ diet they were causing them to produce male offspring and endangering the survival of the species. The mechanisms by which birds exercise facultative control over sex ratio will 1 day be understood using the kind of hierarchical functional role analysis discussed in the previous section. The ultimate system capacity to which these mechanisms contribute, however, will be a conception of survival and reproduction that was not available until the early 1970s when population geneticists showed that selection can act on variance in offspring number as well as on the expected number of offspring.

The capacity of developments in evolutionary theory to change our understanding of what counts as biological functioning is not restricted to traits that are directly involved in reproduction. Apparently straightforward aspects of physiology such as rate of growth and adult body size can only be properly understood in the light of life history theory. For example, it is inaccurate to characterize the broader function of the many biological processes that contribute to development as the reproduction of the adult form of the organism. The broader function to which these processes contribute is the implementation of a life-history strategy involving different allocation of resources to growth, tissue-maintenance and reproduction at each stage in the life-cycle. The idea that development takes an organism from ‘egg to adult’ is a crude approximation to what, in the light of evolution, we now know to be happening.

The idea that every aspect of an organism must be interpreted in the light of its contribution to evolution sounds suspiciously like a commitment to an extreme version of ‘empirical adaptationism’ (Godfrey-Smith 2000). Empirical adaptationism is the claim that every aspect of the organism has been finely tuned by natural selection. But to suppose that I advocate this view is to miss the point entirely. Even if organisms manage all the trade-offs mentioned in the last paragraph very badly, so that they are not particularly well-adapted, managing these trade-offs is what they are doing. A runner who falls far behind and staggers does not thereby transform the race into a staggering contest. To continue the analogy, I am not arguing that all organisms are great runners: I am arguing that they are all in a race.

There is a substantial question about which parts of the physical world, and which properties of those parts, form the subject matter of biology. The examples discussed in this section suggest that any adequate solution to this problem must pay

attention to the role of parts and processes in evolution, as well as their role in the maintenance of the physiological individual. The capacities for ‘self-reproducibility’ and ‘viability’ identified by non-evolutionary accounts of biological functioning represent part but not all of what organisms must do in order to survive and reproduce in the full, evolutionary sense. Non-evolutionary accounts of biological functioning can therefore be seen as special cases of the account to be developed below, an idea I will return to in Sect. 9.

## 7 An Evolutionary Perspective Without Paradox

I have argued that an evolutionary perspective on biological functioning is necessary (Sect. 6) but that the usual interpretation of what constitutes an evolutionary perspective leads to a vicious regress (Sect. 4). This paradox can be avoided by distinguishing two kinds of biological functioning which are privileged from an evolutionary viewpoint, only one of which gives rise to the paradox. This distinction is inspired by two of the four questions in Niko Tinbergen’s famous essay ‘On the Aims and Methods of Ethology’ (1963). Tinbergen suggested that to understand any living organism we need to answer four questions:

1. Causation
2. Survival value
3. Ontogeny
4. Evolution

Questions of causation ask about the mechanisms by which organisms do what they do, and questions of ontogeny ask how those mechanisms are built. Taken collectively these two correspond to Mayr’s (1961) ‘proximal biology’. The important distinction for my purposes, however, is that which Tinbergen draws between ‘survival value’ and ‘evolution’.

Questions of survival value ask: “whether any effect of the observed process contributes to survival if so how survival is promoted and whether it is promoted better by the observed process than by slightly different processes” (1963, p. 118). It is clear in context that Tinbergen understands ‘survival’ in the broad sense of both individual survival to reproductive maturity and reproduction, just as his student Richard Dawkins did when he was inspired by Tinbergen to describe organisms as ‘survival machines’ (Dawkins et al. 1991, p. xii). The study of survival value is simultaneously evolutionary, because it is guided by our best current models of evolution, and ‘methodologically creationist’ in the sense that it is logically independent of past evolution. Tinbergen himself put the point this way “even if the present-day animals were created the way they are now, the fact that they manage to survive would pose the problem of *how they do this*.” (1963, p. 423 my emphasis). Even creationists must study survival value or abandon a key biological question, namely why some populations, and some variants within a population, are increasing in numbers or decreasing or staying constant.

Tinbergen’s fourth question concerns evolution. The study of evolution has “two major aims: the elucidation of the course evolution must be assumed to have taken,

and the unraveling of its dynamics.” (1963, p. 428) The course of evolution is revealed by inferring phylogenies and homologies. The dynamics of evolution are revealed by the study of (1) population genetics and (2) survival value (1963, p. 428), which correspond to the ‘consequence laws’ and ‘source laws’ in Elliot Sober’s (1984) analysis of evolutionary theory. So while evolutionary questions concern the historical trajectory that brought organisms to their present state, questions of survival value concern evolutionary processes going on from moment to moment in current populations.

Tinbergen’s concept of ‘survival value’ opens up the possibility of a genuinely evolutionary perspective that is not an historical perspective, and thus not prone to the vicious regress identified in Sect. 4. Rather than focusing on causal capacities that featured in past episodes of selection, we should focus on causal capacities that contribute to survival and reproduction (survival value). Both of these foci constitute ‘evolutionary perspectives’ on biological functioning. The first identifies biological functioning with parts and processes performing their selected functions. The second identifies biological functioning with parts and processes performing causal functions which contribute to survival and reproduction. The first is a backward-looking evolutionary perspective, seeking to view current organisms in the light of what we know about their evolution. It is because the perspective is backwards-looking that it generates a vicious regress when it is used to define biological functioning. The alternative is a forward-looking evolutionary perspective, seeking to view current organisms in the light of what we know about the evolutionary process. The vicious regress is avoided by adopting this forward-looking evolutionary perspective on the organism. Although this approach asks profoundly evolutionary questions, the answers to those questions are available through experimental analysis of living organisms and their interactions with the environment. As Tinbergen says, it is the “confusion of the study of natural selection with that of survival value” (1963, p. 418) which leads to the mistaken view that survival value cannot be studied by “exact experimentation”.

The fact that the study of survival value is ‘methodologically creationist’ should not be surprising. Any dynamical theory that explains how things change moment by moment can be used both to explain how things are now and to predict how they will be in the future. These two applications of the theory are logically independent. For example, we can use the same physics to explain how the planets got where they are today, given that they were in certain locations yesterday, and to predict where they will be tomorrow, given where they are today. Someone whose religion tells them the planets were created last night will reject this explanation of how they got where they are today. But this bizarre belief does not prevent them using the very same physics to predict where the planets will be tomorrow. In the same way, someone who insists that the world was created a few thousand years ago will reject evolutionary explanations, but the populations they see around them are continually evolving, a fact that has many practical implications from conservation biology to the treatment of epidemic disease. Regardless of their beliefs about the past, a creationist who wants to understand the present will need the full apparatus of evolutionary theory.

## 8 Clarifications and Replies to Objections

1. In earlier work I have criticized the view that biological parts and processes are defined by their selected function on rather different grounds. I argued that it overlooks the central role of homology in biological classification (Griffiths 2006, 2007a, b). This criticism was first made in an important paper by Ronald Amundson and George Lauder, who suggested that a “a glance in any comparative anatomy textbook” should be enough to refute the view that anatomical parts are defined by the function for which they were selected (Amundson and Lauder 1994, p. 453).

I take the arguments in this paper to be consistent with the claim that the fundamental identity of the parts and processes studied in experimental biology is given by homology. Question like ‘which bone is that?’ and ‘which gene is that?’ are answered by classifying those bones and genes by homology. Thus, for example, the long bones which support the wing membrane of a bat are homologous to my fingers. This is part of the answer to the question ‘which bones do bats use to support their wing membranes?’ The single opsin gene on the X-chromosome of a marmoset is homologous to both the medium and long-wave opsin genes on my own X chromosome. This is part of the answer to the question ‘which genes are these ones on the human X chromosome that allow humans to distinguish colours?’ To identify a part or process is to identify which parts it corresponds to in other organisms. Since the 1840s biologists have referred to this relation of correspondence as ‘homology’.<sup>4</sup> Since Darwin they have defined homology as descent from a common ancestor, although in recent years developmental definitions of homology have been proposed. Categories defined by selected function, however, are categories of evolutionary *analogy*. Biologists have traditionally recognized homology and analogy as complementary principles of classification. Analogies potentially unite many different homologues which have some shared feature in their selection history. Thus, for example, the category ‘wing’ is defined by analogy, but the anatomical features of birds, bats, pterosaurs and insects that fall under that category are defined by homology. Different things (homologues) have been adapted in each of these four lineages to become the same thing (analogue).

In this earlier work I also argued that biologists can straightforwardly describe the form and (causal) function of parts and processes, and that this descriptive biology provides the evidence base for claims about both homology and analogy (Griffiths 2007a, see also Winther 2006). The arguments developed in this paper suggest that this descriptive work is guided by evolutionary theory in a more fundamental sense than I had previously realized. This may explain why some earlier philosophers have supposed that even straightforward biological descriptions make implicit claims about the selective history of the relevant parts (Neander 2002; Rosenberg 2001, 2006). This, however, leads to the paradox that I outlined in Sect. 4. If biologists needed to know why something evolved before they could describe its form and function then they could never get of the ground.

<sup>4</sup> Some molecular biologists use the term ‘homology’ to mean sequence similarity, and most molecular biologists refer to different forms of homology, resulting from different copying mechanisms, as ‘orthology’, ‘paralogy’ and ‘xenology’ (on this and other aspects of the homology concept see Brigandt 2002, 2003; Griffiths 2006, 2007a).



2. A common response when I have presented the paradox described in Sect. 4 above is that while biologists cannot *know* the selected function of a part before they describe it, they can *hypothesize* a selected function and this hypothesis helps them describe its form and (causal) function. If we examine this suggestion in more detail, however, it morphs into the alternative, forward-looking heuristic that I have advocated in this paper. Suppose that a biologist examines a stretch of genome or a body part of a little-studied organism. They can draw on no prior understanding of the role this part plays in the life of the organism, or even whether it really is part of the organism, as opposed to a parasite. So they have to face the questions identified by Millikan (Sect. 3). Can it seriously be suggested that the *first* thing they should do is to hypothesize that the part evolved because of a particular set of selection pressures? What reason could there be to choose one selection pressure rather than another, given that nothing is known about the form and function of the part? Instead, I think what people have in mind here is that the initial descriptive biology is a search for how the part contributes to the organism’s survival and reproduction. It is guided by previously researched examples of how parts contribute to survival and reproduction. If it can be established that the newly discovered part makes some such contribution, then this may very well be why the part evolved. However, it was not that historical hypothesis that played the heuristic role in the initial description of the system, but the idea of looking for contributions to survival and reproduction and for distinctive kinds of contribution that are familiar from other organisms. In other words, it is the forward-looking evolutionary perspective that guides an initial biological description, not the backward-looking evolutionary perspective.

3. Another common response is that, since the forward-looking evolutionary perspective must be applied to organisms in their ‘natural habitat’ and this, it is argued, can only mean their historical habitat, there is no real difference between the forward-looking and backward-looking perspective. I am not convinced that the premise of this argument is correct. So-called ‘invasion biology’ studies how introduced organisms survive all too well in environments that are definitely not those in which they evolved. Invasion biologists successfully answer Tinbergen’s question ‘how do they do this?’ and they do not seem to face insuperable problems in defining biological functioning. But it does seem to be true that, for example, it is more illuminating to study a lion on the savannah than a lion in a cage, and this is something I need to explain. I suggest that there are two, independent reasons why explanations of how organisms survive and reproduce in historically normal environments are more illuminating than explanations of how they survive and reproduce (if they do) in novel environments. First, in many novel environments organisms do not work very well, and it is typically more interesting to understand how a mechanism achieves some impressive feat of natural engineering than how it barely gets by or fails outright. When an organism does spectacularly well in a novel environment, however, like the Cane Toad so catastrophically introduced to Australia, it can be very interesting to understand how it does so well. Second, one of the main reasons for studying survival value is to go on to answer Tinbergen’s fourth, evolutionary question. Understanding how organisms survive and reproduce in their historically normal environment is more relevant to this further question than understanding how they perform in novel environments. Both of these ideas are

consistent with my claim that it is the forward-looking evolutionary perspective that actually guides biological research. In the case of the lion, what is studied in the natural, savannah habitat, or in a model of that habitat, is how the parts of the lion causally contribute to survival and reproduction. This research is guided by exemplars of how parts contribute to survival and reproduction in other organisms or other models. The results provide support for hypotheses about how the parts evolved (selected function). None of this involves the paradox-inducing appeal to historical information discussed in Sect. 4.

4. After presenting this material at conferences I have encountered a number of objections which identify something about the actual selective history of an organism that, in conjunction with some other facts, can form part of an argument for or against some hypothesis about form or causal function in that organism. The objectors take this to refute my view. But the arguments presented above do not commit me to the extreme position targeted by such objections. I have identified one pattern of argument in which claims about selected function are used to support claims in proximal biology, a pattern which earlier authors have suggested is extremely important (Sect. 3). I have pointed out that this pattern of reasoning leads to a vicious regress (Sect. 4). I have suggested a way to do without it (Sect. 7). This does not imply that that nothing we might know about the selective history of organisms could play a role in any argument for any claim in proximal biology!

5. Given the prominence of the debate over ‘adaptationism’ in evolutionary biology (Dupré 1987; Gould and Lewontin 1978; Orzack and Sober 2001) I should clarify how the arguments of this paper relate to that debate. Peter Godfrey-Smith has distinguished three kinds of ‘adaptationism’ (Godfrey-Smith 2000). ‘Empirical adaptationism’ is the thesis that almost all aspects of organisms are finely tuned by natural selection. The approach to defining biological functioning that I have defended here does not assume empirical adaptationism. Even if organisms were highly constrained in their ability to respond to selection, biologists could still answer Tinbergen’s question about ‘survival value’ and could still define biological functioning using the forward-looking evolutionary heuristic. Biological functioning would still be a matter of survival and reproduction, but organisms would not be as good at surviving and reproducing as an enthusiastic empirical adaptationist might suppose.

Godfrey-Smith identifies two other forms of adaptationism. ‘Methodological adaptationism’ makes no commitments about how well-adapted organisms are, but contends that the study of adaptation is the best way to identify both adaptations and constraints on adaptation. ‘Explanatory adaptationism’ contends that the adaptation of organisms to their environment is the primary thing that biologists should seek to explain. It seems intuitively plausible that the approach to defining biological functioning that I have defended here might lend support to either of these two theses, but I do not have any substantive arguments to link them, and it may be that this intuition is misguided.

6. While the arguments in this paper are in some danger of being condemned as excessively adaptationist, they are equally likely to be pilloried as ‘anti-evolutionary’. So let me reiterate that I am not suggesting we cannot or should not study how particular organisms actually evolved. My point is that the success of such studies

for any particular species is not and cannot be a necessary precursor to successful work on the ‘proximal’ biology of that species.

## 9 Summary and Conclusions

Millikan and others have identified a genuine problem with the definition of biological functioning. Although it is easy to overlook it once the problem has been solved, the proximal biology of organisms needs to be conducted against a background of assumptions about where one organism ends and the next begins, about the range of conditions under which the organism is actually functioning as opposed to participating in irrelevant causal processes such as burning in a forest fire, and about which traits need to be studied as part of the organisms functioning as opposed to part of its malfunctioning (pathology). The fact that sperm are part of our reproductive machinery was not obvious to those who discovered them, nor was the purpose for which they rotate their flagella. Just which features of sperm morphology are pathological remains in dispute today.

The consensus that these problems are solved by examining the selective history of the parts and processes that make up organisms has come under attack in recent years. Proximal biologists often do not have the data needed to establish evolutionary scenarios for the mechanisms they study, and they typically make no effort to obtain it. This has led several philosophers and biologists to argue that biologists answer Millikan’s questions in other ways. These non-evolutionary accounts identify a general causal capacity, such as ‘viability’ or ‘self-reproduction’, that defines biological functioning. These causal capacities are ahistorical properties of actual organisms, and so whether a part or process contributes to such a capacity is something that can be ascertained by experimental investigation. This ahistorical, non-evolutionary account seems to fit better with how biologists actually approach these questions.

I have offered a more principled objection to the conventional, backward-looking evolutionary definition of biological functioning. If we cannot describe the biological functioning of an organism without understanding why it evolved, then we will face a vicious regress, since the only way to understand why it evolved is to describe the biological functioning of its ancestors.

I have rejected existing ahistorical, non-evolutionary definitions of biological functioning, however, on the grounds that many aspects of the biological functioning of organisms can only be understood as mechanisms contributing to the evolutionary success of the organisms. In their place I have offered an ahistorical but still evolutionary definition. All and only those parts and processes that contribute to the capacity of an organism for survival and reproduction, construed in terms of our current best theory of evolutionary dynamics, are aspects of its biological functioning. Millikan’s question about where one organism ends and another begins is the well-known question of the units of evolution. Millikan’s questions about which causal processes are part of biological functioning and which are irrelevant is answered by determining which processes are part of the explanation of how organisms survive and reproduce. Millikan’s question about what is pathology and what ‘normal’ variation is answered in the same way. Answering each of these questions is hard, and the quality

of our answers will reflect how well we understand the evolutionary process. In Sect. 6 I described some aspects of biological functioning that were ‘invisible’ until the relevant developments in evolutionary theory. These include the biology of aging, and life history strategy more generally, and aspects of reproductive biology such as the facultative control of sex ratio. Further advances in understanding evolution will have a similar, transforming effect on our understanding of biological functioning.

The new evolutionary perspective that I propose can be seen as a ‘friendly amendment’ to the non-evolutionary accounts or to accounts like Wouters (2007) that are not explicitly non-evolutionary, but which do not emphasize the analysis of reproductive fitness. The fact that ‘experimental’ (Weber 2005) or ‘functional’ (Wouters 2007) biology is framed by an evolutionary perspective has not been apparent to some authors, I believe, because much of this research is still documenting basic mechanisms and its conclusions are not yet detailed enough to require an exact specification of the causal capacity to which these mechanisms contribute. For the purpose of elucidating the general mechanisms of nervous transmission, for example, the theory that organisms have the ultimate goal of just staying alive is as good as the theory that they have the ultimate goal of survival and reproduction. Much of functional biology studies causal roles that would be common ground even between Darwinians and creationists. No creationist would demur at the suggestion that God’s purpose in creating calcium channels in the walls of neurons was that they should play a role in the generation and transmission of nerve impulses. A forward-looking evolutionary perspective will give the same answer as the non-evolutionary perspective in many cases. It is superior because there are test cases where the non-evolutionary perspective breaks down.

The forward-looking evolutionary perspective achieves this superiority because it embodies the advances in our understanding of biological functioning that have been produced by the theory of evolution. Advances such as Darwin’s concept of sexual selection or post-Hamiltonian ideas about life history give us a better understanding of what is going on when we look at an organism. If we understand evolutionary theory, then we can see things that were invisible to earlier biologists. This is shown dramatically by the example of the Kakapo’s reproductive strategy given in Sect. 6. But in contrast to the conventional idea that it is our understanding of the specifics of evolutionary history that provides this insight, I have argued that our understanding of evolution influences our understanding of biological functioning by contributing to our general grasp of what it is to evolve and thus of what it is to function. Success in understanding how evolution shapes the characters of organisms enriches our understanding of the kinds of mechanisms that can affect the future evolutionary trajectory of populations, and thus our understanding of biological functioning.

## References

- Amundson R, Lauder GV (1994) Function without purpose: the uses of causal role function in evolutionary biology. *Biol Philos* 9(4):443–470. doi:[10.1007/BF00850375](https://doi.org/10.1007/BF00850375)

- Bigelow J, Pargetter R (1987) Functions. *J Philos* 54:181–196. doi:[10.2307/2027157](https://doi.org/10.2307/2027157)
- Bock WJ, von Wahlert G (1965) Adaptation and the form-function complex. *Evolution* 19:269–299. doi:[10.2307/2406439](https://doi.org/10.2307/2406439)
- Brandon RN (1981) Biological teleology: questions and explanations. *Stud Hist Philos Sci* 12:91–105. doi:[10.1016/0039-3681\(81\)90015-7](https://doi.org/10.1016/0039-3681(81)90015-7)
- Brigandt I (2002) Homology and the origin of correspondence. *Biol Philos* 17:389–407. doi:[10.1023/A:1020196124917](https://doi.org/10.1023/A:1020196124917)
- Brigandt I (2003) Homology in comparative, molecular and evolutionary biology. *J Exp Zool (Mol Dev Evol)* 299B:9–17. doi:[10.1002/jez.b.36](https://doi.org/10.1002/jez.b.36)
- Burian RM (2005) *The epistemology of development, evolution, and genetics*. Cambridge University Press, Cambridge
- Canfield J (1964) Teleological explanation in biology. *Br J Philos Sci* 14:285–295. doi:[10.1093/bjps/XIV.56.285](https://doi.org/10.1093/bjps/XIV.56.285)
- Christensen W (1996) A complex systems theory of teleology. *Biol Philos* 11(3):301–319. doi:[10.1007/BF00128784](https://doi.org/10.1007/BF00128784)
- Clout MN, Elliott GP, Robertson BC (2002) Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. *Biol Conserv* 107(1):13–18. doi:[10.1016/S0006-3207\(01\)00267-1](https://doi.org/10.1016/S0006-3207(01)00267-1)
- Cummins R (1975) Functional analysis. *J Philos* 72:741–765. doi:[10.2307/2024640](https://doi.org/10.2307/2024640)
- Cummins R (1983) *The nature of psychological explanation*. Bradford/MIT, Cambridge
- Davies PS (2001) *Norms of nature: naturalism and the nature of functions*. MIT Press, Cambridge
- Dawkins MS, Halliday TR, Dawkins R (eds) (1991) *The Tinbergen legacy*. Chapman and Hall, London
- Delancey C (2006) Ontology and teleofunctions. *Synthese* 150:69–98. doi:[10.1007/s11229-004-6257-8](https://doi.org/10.1007/s11229-004-6257-8)
- Diamond J (1982) Big-bang reproduction and ageing in male marsupial mice. *Nature* 298(5870):115–116. doi:[10.1038/298115a0](https://doi.org/10.1038/298115a0)
- Diamond J (1997) *Guns, germs, and steel: the fates of human societies*. W. W. Norton & Company, New York
- Dobzhansky T (1973) Nothing in biology makes sense except in the light of evolution. *Am Biol Teach* 35:125–129
- Dupré J (ed) (1987) *The latest on the best: essays on optimality & evolution*. MIT Press, Cambridge
- Edin BB (2008) Assigning biological functions: making sense of causal chains. *Synthese* 161(2):203–218. doi:[10.1007/s11229-007-9160-2](https://doi.org/10.1007/s11229-007-9160-2)
- Gasking EB (1967) *Investigations into generation, 1651–1828*. Johns Hopkins Press, Baltimore
- Gintis H (2007) Book Review: David J. Buller. 2005. *Adapting minds: evolutionary psychology and the persistent quest for human nature*. *J Bioeconomics* 9(2):191–200. doi:[10.1007/s10818-007-9023-4](https://doi.org/10.1007/s10818-007-9023-4)
- Godfrey-Smith P (1993) Functions: consensus without unity. *Pac Philos Q* 74:196–208
- Godfrey-Smith P (1994) A modern history theory of functions. *Noûs* 28:344–362
- Godfrey-Smith P (2000) Three kinds of adaptationism. In: Orzack S, Sober E (eds) *Optimality and adaptation*. Cambridge University Press, Cambridge, pp 335–357
- Gould SJ, Lewontin R (1978) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc R Soc Lond B Biol Sci* 205:581–598
- Gould JA, Vrba ES (1982) Exaptation—a missing term in science of form. *Paleobiology* 8:4–15
- Griffiths PE (1992) Adaptive explanation and the concept of a vestige. In: Griffiths PE (ed) *Trees of life: essays in philosophy of biology*. Kluwer, Dordrecht, pp 111–131
- Griffiths PE (1993) Functional analysis & proper function. *Br J Philos Sci* 44:409–422. doi:[10.1093/bjps/44.3.409](https://doi.org/10.1093/bjps/44.3.409)
- Griffiths PE (2006) Function, homology and character individuation. *Philos Sci* 73(1):1–25. doi:[10.1086/510172](https://doi.org/10.1086/510172)
- Griffiths PE (2007a) The phenomena of homology. *Biol Philos* 22(5):643–658. doi:[10.1007/s10539-007-9090-x](https://doi.org/10.1007/s10539-007-9090-x)
- Griffiths PE (2007b) Evo-Devo meets the mind: towards a developmental evolutionary psychology. In: Sansom R, Brandon RN (eds) *Integrating development and evolution*. MIT Press, Cambridge, pp 195–225
- Lewens T (2004) *Organisms and artifacts: design in nature and elsewhere*. MIT Press, Cambridge
- Lorenz KZ (1966) Evolution of ritualisation in the biological and cultural spheres. *Philos Trans R Soc Lond* 251:273–284. doi:[10.1098/rstb.1966.0011](https://doi.org/10.1098/rstb.1966.0011)
- Mayr E (1961) Cause and effect in biology. *Science* 131:1501–1506. doi:[10.1126/science.134.3489.1501](https://doi.org/10.1126/science.134.3489.1501)

- McLaughlin P (2001) What functions explain: functional explanation and self-reproducing systems. Cambridge University Press, Cambridge
- Millikan RG (1984) Language, thought and other biological categories. MIT Press, Cambridge
- Millikan RG (2002) Biofunctions: two paradigms. In: Cummins R, Ariew A, Perlman M (eds) Functions new readings in the philosophy of psychology and biology. Oxford University Press, Oxford, pp 113–143
- Moore HDM, Martin M, Birkhead TR (1999) No evidence for killer sperm or other selective interactions between human spermatozoa in ejaculates of different males in vitro. *Proc R Soc Biol Sci* 266(1436):2343–2350. doi:[10.1098/rspb.1999.0929](https://doi.org/10.1098/rspb.1999.0929)
- Nahvi A, Sudarsan N, Ebert MS, Zou X, Brown KL, Breaker RR (2002) Genetic control by a metabolite binding mRNA. *Chem Biol* 9(9):1043–1049. doi:[10.1016/S1074-5521\(02\)00224-7](https://doi.org/10.1016/S1074-5521(02)00224-7)
- Neander K (1991a) Functions as selected effects: the conceptual analyst's defense. *Philos Sci* 58:168–184. doi:[10.1086/289610](https://doi.org/10.1086/289610)
- Neander K (1991b) The teleological notion of “function”. *Australas J Philos* 69(4):454–468. doi:[10.1080/00048409112344881](https://doi.org/10.1080/00048409112344881)
- Neander K (2002) Types of traits: the importance of functional homologues. In: Ariew A, Cummins R, Perlman M (eds) Functions: new essays in the philosophy of biology and psychology. Oxford University Press, Oxford
- Orzack S, Sober E (eds) (2001) Optimality and adaptation. Cambridge University Press, Cambridge
- Papineau D (1987) Reality and representation. Blackwell, New York
- Pigliucci M, Kaplan JM (2006) Making sense of evolution: the conceptual foundations of evolutionary theory. University of Chicago Press, Chicago
- Pittendrigh CS (1958) Adaptation, natural selection and behavior. In: Roe A, Simpson GG (eds) Behavior and evolution. Yale University Press, New Haven, pp 390–416
- Rosenberg A (2001) The character concept: adaptationalism to molecular developments. In: Wagner GP (ed) The character concept in evolutionary biology. Academic Press, San Diego, pp 201–216
- Rosenberg A (2006) Darwinian reductionism or, how to stop worrying and love molecular biology. University of Chicago Press, Chicago
- Schlösser G (1998) Self re-production and functionality: a systems-theoretical approach to teleological explanation. *Synthese* 116:303–354. doi:[10.1023/A:1005073307193](https://doi.org/10.1023/A:1005073307193)
- Sober E (1984) The nature of selection: evolutionary theory in philosophical focus. MIT Press, Cambridge
- Tinbergen N (1963) On the aims and methods of ethology. *Z Tierpsychol* 20:410–433
- Weber M (2005) Philosophy of experimental biology. Cambridge University Press, Cambridge
- Wimsatt WC (1972) Teleology and the logical structure of function statements. *Stud Hist Philos Sci* 3:1–80. doi:[10.1016/0039-3681\(72\)90014-3](https://doi.org/10.1016/0039-3681(72)90014-3)
- Wimsatt WC (2007) Re-engineering philosophy for limited beings: piecewise approximations to reality. Harvard University Press, Cambridge
- Winther RG (2006) Parts and theories in compositional biology. *Biol Philos* 21(4):471–499. doi:[10.1007/s10539-005-9002-x](https://doi.org/10.1007/s10539-005-9002-x)
- Wouters A (1995) Viability explanation. *Biol Philos* 10(4):435–457. doi:[10.1007/BF00857593](https://doi.org/10.1007/BF00857593)
- Wouters A (2003) Four notions of biological function. *Stud Hist Philos Biol Biomed Sci* 34:633–668. doi:[10.1016/j.shpsc.2003.09.006](https://doi.org/10.1016/j.shpsc.2003.09.006)
- Wouters A (2005a) The functional perspective in evolutionary biology. In: Reydon TAC, Hemerik L (eds) Current themes in theoretical biology. Springer, Berlin, pp 33–69
- Wouters A (2005b) The functions debate in philosophy. *Acta Biotheor* 53:123–151. doi:[10.1007/s10441-005-5353-6](https://doi.org/10.1007/s10441-005-5353-6)
- Wouters A (2007) Design explanation: determining the constraints on what can be alive. *Erkenntnis* 67(1):65–80. doi:[10.1007/s10670-007-9045-2](https://doi.org/10.1007/s10670-007-9045-2)