



New challenges to the selected effects account of biological function

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Abstract

Finding a naturalistic account of biological function is important both for making sense of the way functions are talked about in biology and medicine and for the project in the philosophy of mind of naturalising mental content via teleosemantics. The selected effects theory accounts for the proper functions of traits in terms of their selectional history, and is widely considered to be the most promising approach to naturalising biological functions. However, new challenges to the selected effects account have recently emerged. Matthewson (2020) argues that natural selection comes in degrees and that on the face of it biological function does not, suggesting that analysing the latter in terms of the former is therefore problematic. Christie et al. (forthcoming) argue that the selected effects account of function does not fit with biologically detailed accounts of actual selection processes, in that it focuses on the functions of traits of individuals rather than the frequency of traits in populations and does not generate accurate selectional explanations in cases in which there is not a uniform selective environment. This paper defends the selected effects account against these challenges, arguing that a viable response to Matthewson is that *any* degree of selection suffices to confer proper functions, and that Christie et al. mischaracterise the aims and assumptions of the selected effects account.

Keywords Biological function · Selected effects · Natural selection · Proper function

1 Introduction

A naturalistic account of biological function is important both for making sense of the way functions are talked about in biology and medicine and for the project in the philosophy of mind of naturalising mental content via teleosemantics. The selected effects theory [see for example (Neander, 1991); (Millikan, 1984, 1989b); (Griffiths,

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1993); (Godfrey-Smith, 1994)] accounts for the proper functions of traits in terms of their selectional history, and is widely considered (at least in Anglophone philosophy of biology) to be the most promising approach to naturalising biological proper functions [see for example (Rubner, 2022); (Allen & Neal, 2020)]. Recently, however, the scientific credentials of the selected effects account have been challenged. Matthewson (2020) argues that natural selection comes in degrees and that on the face of it biological function does not, suggesting that analysing the latter in terms of the former is therefore problematic. Christie et al. (forthcoming) argue that the selected effects account of function does not fit with biologically detailed accounts of actual selection processes, in that it focuses on the functions of traits of individuals rather than the frequency of traits in populations and does not generate accurate selectional explanations in cases in which there is not a uniform selective environment. This paper defends the selected effects account against these challenges, arguing that a viable response to Matthewson is that *any* degree of selection suffices to confer proper functions, and that Christie et al. mischaracterise the aims and assumptions of the selected effects account.

2 Proper functions in biology and the philosophy of mind

The proper function of a thing is what that thing is for: what it is in some sense *supposed to* do. Artefacts have proper functions: hammers are for banging in nails, can-openers are for opening cans. Biological items also have proper functions: hearts are for pumping blood, sperm are for fertilising ova.

It is a feature of proper functions that a thing can have a proper function that it does not perform, either because it is broken or because it is not in the right circumstances for performing it. A bent and twisted can-opener still has the function of opening cans even if it cannot be made to do so; most sperm are never in a position to fertilise an ovum, but that is still their function. That is to say, the proper function of a particular item is not always something that it actually does.

Another feature of proper functions is that not everything an item does counts as its proper function. Hearts make a certain kind of noise in the process of pumping blood, and occupy a space in the chest cavity, but it is pumping blood rather than making that noise or occupying that space that is their proper function. Perhaps my child has been using my can-opener to bang in nails: even if a particular can-opener *does* bang in nails, doing so is not its proper function. This is the function/accident distinction: some of the things (even some of the useful things) done by a trait or by an artefact are not its proper functions, but rather things it just happens to do.

The function/accident distinction goes along with a particular explanatory role that proper functions play: the proper function of a thing can be used to explain why the thing is present, or why it is the way it is, while an accidental feature of the thing cannot. Why is there a can-opener in my kitchen drawer? In order to open cans (not in order to bang in nails, even if it can be used for this purpose). Why do I have a heart? In order to pump blood (not in order to make certain noises, though my heart does that as well).

These are teleological explanations, and on the face of it they are puzzling. How can my heart's function explain its presence? At first glance, this looks like backwards causation—my heart's presence is explained by an activity that postdates its coming into existence. At second glance, it looks like creationism. Can-openers get their functions from the intentions of their creator or designer. There is a can-opener in my drawer because someone designed it for opening cans and because I need something that will open cans—there is no backwards causation, only designer and user intentions. In more creationist times, biological functions were also thought of in this way: my heart was thought to be for pumping blood because pumping blood is what a creator/designer intended it to do. Some think that proper function talk and teleological explanation in biology are the residue of creationism, and that the right response to the discovery of evolution by natural selection is to eliminate them (Cummins, 1975; Ratti & Germain, 2022); others (in particular selected effects theorists) think that Darwinism instead provides a basis for naturalising biological teleology (Neander, 2017a).

Proper functions play several key roles in biology and medicine, and it would be problematic if there was no naturalistic account of them. The distinction between well-functioning and malfunctioning organs or systems depends on the ascription of proper functions to those organs or systems. Additionally, it is arguable (see for example (Matthewson & Griffiths, 2017) that the concept of *disease*, whether or not it can be analysed solely in terms of biological malfunction, at least has biological malfunction as a component. Finally, evolutionary biologists explain why an organism has the traits that it has in terms of what those traits are *for*: we have hearts for pumping blood, and the fact my heart has that function explains why I have one.

There may be other kinds of function-talk in biology—for example, Robert Cummins (Cummins, 1975) thinks of the function of a component of a biological system as the causal role it plays in that system, and others have proposed a kind of pluralism about biological function, some biological functions being proper functions and others being Cummins-functions [see for example (Godfrey-Smith, 1993)]. However, the uses of functions mentioned above—distinguishing between function and malfunction, and explaining the presence of a trait in terms of its function—require those functions to be proper functions; not just things that biological items in fact do, but what they are for.

In the philosophy of mind, one of the most promising routes towards naturalising intentionality (aboutness) is teleosemantics, which accounts for mental content in terms of proper function. Teleosemanticists such as Karen Neander (1995a, 2017b) and David Papineau (1987, 1993) think the function of a mental state like a belief is to carry information about a particular state of affairs, and the content of the mental state is the state of affairs it has the proper function of carrying information about. An alternative teleosemantic theory, that of Ruth Millikan (1984, 1986, 1989a) has it that the proper function of an indicative mental state like a belief is to participate in inferences that lead to behaviour that satisfies the believer's desires, and the content of the belief is a state of affairs that has normally obtained when the belief has succeeded in performing that function. Teleosemantics is more promising than competing attempts to naturalise intentionality because the appeal to proper functions enables it to straightforwardly explain *misrepresentation*: a belief can have a proper function that it fails to perform, and a belief can be tokened in the absence of the conditions that have in the past enabled

it to perform its proper function. Teleosemantics will only count as a naturalistic account of intentionality, however, if we have a naturalistic account of proper function in place, and all of the above-mentioned teleosemanticists endorse a selected effects account of proper function.

All of these uses of proper function require proper functions to be objective: when we say that something has a proper function, we are not merely saying something about our own interests or goals.

3 The selected effects account of proper function

The dominant naturalistic account of proper function, amongst teleosemanticists and more generally, is the selected effects account.¹ On this account, the proper function of a trait is what ancestral instances of the trait have done to contribute to the enhanced survival and reproduction (relative to competitors) of the ancestors of the current trait-holder. Given that the trait is passed on from generation to generation, this means that the fact that ancestral instances performed this proper function is part of the explanation of why the current trait-holder has that trait. For example, the proper function of my heart is to pump blood because pumping blood is what the hearts of my ancestors did that contributed to their fitness, and this partially explains why my heart is the way it is.

Here is Ruth Millikan's version of the selected effects account:

- [F]or an item A to have a function F as a “proper function,” it is necessary (and close to sufficient) that... A originated as a “reproduction” (to give one example, as a copy, or a copy of a copy) of some prior item or items that, due in part to possession of the properties reproduced, have actually performed F in the past, and A exists because (causally historically because) of this or these performances.
- (Millikan, 1989b, p. 288).

Millikan's account applies equally to biological traits and to artefacts that have been subject to a selection process. Karen Neander's version of the selected effects account is biology-specific:

- It is a/the proper function of an item (X) of an organism (O) to do that which items of X's type did to contribute to the inclusive fitness of O's ancestors, and which caused the genotype, of which X is the phenotypic expression, to be selected by natural selection.
- (Neander, 1991, p. 74).

I will use Neander's account here, as the criticisms put forward by Matthewson and Christie et al. focus on issues to do with natural selection and Neander's account makes the role of natural selection explicit. However, the same responses to these criticisms can be made on behalf of Millikan's account.²

¹ This is true in particular in Anglophone philosophy of biology, although there is not complete consensus even there: see Garson (2016) for an overview.

² Amongst others, Paul Griffiths (1993) and Peter Godfrey-Smith (1994) also give selected effects accounts of proper function. Godfrey-Smith adds to the Millikan/Neander view the proviso that the trait a function is

It is generally considered a virtue of the selected effects account that it is scientifically respectable: it accounts for functions in terms of natural selection, and natural selection is a central posit of current biology. However, recent papers by John Matthewson (2020) and by Christie et al. (forthcoming) question whether the selected effects account actually deserves this credit. As Matthewson puts it: “Given that the selected effects account of function relies on the action of natural selection, this account... must be sensitive to features of natural selection itself.” (8) Both Matthewson and Christie et al. suggest that extant versions of the selected effects theory are not: both point out ways in which they think the view of natural selection that the selected effects account relies on is over-simplified.

4 Matthewson’s challenge

Natural selection, Matthewson suggests, is a matter of degree. However, having a proper function is usually treated as something that is *not* a matter of degree: something either has a particular proper function or it doesn’t. Matthewson concludes that at the very least there is some work to be done by those who want to analyse proper function (an ungraded concept) in terms of natural selection (a graded process).

Matthewson uses several different kinds of case to illustrate his claim that natural selection comes in degrees. First, different traits may have been subject to different degrees of selection pressure. For example, there has been selection for hairy nostrils (the hairs keep out airborne particles that might otherwise cause respiratory problems), but this pressure is not as strong as, for example, the selection pressure on the ability of the CFTR channel to transport chloride ions across cell membranes. Individuals with cystic fibrosis lack this, and it is immensely more fitness-reducing than a lack of nostril hairs. As Matthewson says: “Selection has acted on both CFTR cell gates and nose hairs in our ancestors. It has just acted on these traits with differing strengths. So natural selection isn’t merely present or absent; it comes in degrees.” (Matthewson, 2020, p. 5). In a second kind of case, some populations are such that there is not intense competition for resources amongst individuals, although there is *some* competition. For example, consider a small population in a large area with plenty of food available, but not *so* much food that every individual can have as much as would benefit them. In such a population, although there will be selection in favour of traits that help an individual get food, the selection will be less intense than it would be in an environment where food is scarcer. Again, cases like this show that the force of natural selection comes in degrees.

Matthewson also discusses cases that involve changes in the direction of selection due to environmental changes. For example, in the peppered moth, whether dark pigmentation or light pigmentation is being selected for at a particular time depends

Footnote 2 continued

being attributed to must have contributed to the fitness of its possessors *in the recent past* (359). Griffiths’ account is similar to Godfrey-Smith’s, but unlike Godfrey-Smith, Millikan and Neander, Griffiths defines what it is for a trait-*type* rather than a trait-*token* to have a biological function. A corollary of this is that on Griffiths’ account, the present-day state of affairs that is explained by a function-attribution is not an individual’s possession of a trait, but the non-zero proportion of a trait in a current population. This is also a feature of the “canonical” account proposed (although not endorsed) in (Christie et al., forthcoming), to be discussed below.

on the coloration of the tree trunks that it is fitness-enhancing for the moth to match, and that may change depending on the amount of soot human activity is releasing into the air. I will discuss this case in the next section, in conjunction with other cases raised by Christie et al. in which the environment in which selection occurs is heterogeneous. It is less clearly an illustration of Matthewson's point that natural selection comes in degrees than the cases in which some *traits* are more strongly selected for than others and the cases in which traits in some *populations* are subject to greater selection pressure than the same traits in other populations.

Matthewson's examples illustrate the point that a trait is not simply selected for or not: natural selection comes in degrees. Matthewson argues that if proper function attributions are binary rather than graded, the selected effects theorist needs to explain how they get binary function-attributions out of natural selection that comes in degrees. The selected effects theorist, he suggests, needs to find a biologically principled cut-off point between selective force that confers proper functions and selective force that is not strong enough to do so. This threshold needs to be biologically based, rather than being a matter of convention or dependent on our interests, or the objectivity of function-ascriptions will be lost. If the selected-effects theorist cannot do this, then, Matthewson suggests, they should accept that proper functionhood is also a matter of degree—but then they will need to consider how that plays out in theories (such as teleosemantics) that depend on proper functions.

Matthewson thinks that the selected effects theorist will have to take the latter route, because although there are any number of places where we could *pragmatically* draw a line between traits that have been sufficiently strongly selected for to ground a function attribution and traits that have not, there is no biologically-principled place to draw that line. However, I suggest that there is one principled place to draw the line: we might say that *any* degree of selection suffices to confer a proper function.

Note that all proponents of the selected effects account acknowledge that a trait can have more than one proper function. Neander, for example, is defining what it is for something to be “the/a proper function of an item (X) of an organism (O)... “. This formulation acknowledges that a particular trait may not have a unique proper function. That, it seems to me, is already a step towards acknowledging that functions can be grounded in selection processes of differing force. There has presumably never been any reason to think that when you have a trait with multiple functions, all of those functions have been equally selectively important, and yet that has not been taken to undermine the status of any of them as functions.

That is a long way, however, from the claim that *any* contribution of a trait to ancestral fitness, however small, provides the basis for a function-attribution. Matthewson thinks this claim is implausible: “hugely many phenotypic features are likely to have at least minimally enhanced fitness some of the time for some ancestor(s), in which case this rule would greatly over-generate a vast array of full proper functions.” (p. 11).

Matthewson does not seriously consider this option, but I think it is worth considering. Why would it be a problem if there are many more proper functions than we usually think there are? We aren't usually *interested* in functions arising from very small contributions to fitness, but, you might think, that does not mean that they do not exist. The suggestion is not that our interests determine whether or not something is a proper function, but only that they make a difference to which proper functions

(selected effects) we pay attention to. This is a common situation to be in with respect to causal explanations - and selected effects explanations are causal explanations. The causal sequence that leads to a present-day state of affairs is immensely complex, and we do not in general think that we need to pay attention to every detail when we are providing an explanation of how a present-day state of affairs came about. In the kind of case at hand, that means that if there are multiple different things a trait has contributed to ancestral fitness and some have contributed more than others, we might not pay attention to (and might not even notice) the ones that have contributed only a little—but arguably they may still be proper functions of the trait.

Matthewson considers some problems with the view that there is a vast array of *partial* proper functions, and some of these problems potentially also arise for the current suggestion (that there is a vast array of *full* proper functions). Matthewson points out that if there are many more functions that we think, we will seldom be justified in *denying* that a thing has a particular function (p. 13). The very examples that motivated us to distinguish between proper functions and accidental effects are undermined—who is to say that the fact that the hearts of my ancestors made a certain sort of noise never contributed, even a miniscule amount, to their fitness? And, as Matthewson points out, if we want to define disease in terms of dysfunction, the multiplication of functions generates a whole new range of ways in which a biological item can *fail* to perform one of its proper functions (pp. 14–15).

Matthewson thinks of this as in part a practical problem. Part of his aim in defending an account of disease that has biological dysfunction as a component is to restrict what can be classified as a disease, to avoid the pathologising of a range of conditions and behaviours that are societally disapproved of (for example *drapetomania*, a supposed mental illness that caused slaves to run away from their masters) but have no biological basis (pp. 3, 14–15). However, it is not clear that this problem will genuinely arise. If the functions in question are contributions to ancestral fitness so small that they have not previously been noticed, it seems unlikely that they will now be called into play as justifications for claims of biological dysfunction. Perhaps this is in fact less of a problem for my suggestion that any degree of selection grounds the attribution of a fully-fledged proper function than it is for Matthewson's suggestion that there are partial functions, since my suggestion does not require any modification to extant statements of the selected effects account of proper function, and so will not tend to lead would-be pathologists to seek out minor contributions to ancestral fitness of supposed mental disorders.

Whether or not the proliferation of functions is a practical problem, it does on the face of it look like a theoretical problem. Tracking the distinction between what a trait is for and its accidentally useful contributions is the point of an account of proper function. If even a tiny contribution to ancestral fitness suffices for functionhood, the point of proper function ascriptions may be lost.

Suppose that the limiting case of individual I's trait T having the function F is that an ancestor of I's with trait T outreproduced its competitors because T did F and I's competitors did not have T (and T is heritable, so this partially explains why

I has T).³ Many of the classic examples of useful effects that are accidents rather than functions continue to count as accidents even if proper function is considered to have this broad scope. The Bible in the soldier's breast-pocket that stops a bullet still does so accidentally rather than having the function to do so, and does not generate descendant functions unless carrying a Bible in your breast pocket is a heritable trait. If we make the example one in which it *does* look like a heritable trait—for example, the family tells the story of great-grandfather's lucky escape, and form a tradition of always carrying a Bible in their breast pockets—then it starts to look like a trait with a proper function after all. In either case, this is not a counterexample. Or, consider the useful but not proper-functional ability of noses to enable the wearing of spectacles. The current suggestion does not make this come out as a proper function, because there have not been noseless individuals being outreproduced because they didn't have a way of keeping their spectacles on. These examples do not show that the current suggestion draws the function/accident distinction in the right place—much more work would be needed to do that. However, they do go some way towards undermining the worry that this suggestion makes *every* useful thing a trait does turn out to be a proper function.

Is the proliferation of proper functions that have made a very small contribution to ancestral fitness a problem for teleosemantics? It appears not—at least, not for Ruth Millikan's version of teleosemantics. For Millikan, the proper functions of beliefs include playing a particular role in inferences and thus contributing to the satisfaction of desires, and the Normal conditions for the performance of these functions are the conditions that have mostly obtained on the occasions on which the functions have been performed.⁴ The *content* of a belief, for Millikan, is some part of the Normal conditions for the belief's performing these proper functions. My belief that I can get coffee at Stacey's is likely to contribute to the satisfaction of my desire for coffee only if there actually is coffee at Stacey's: there being coffee at Stacey's is a Normal condition for the belief's performing its proper function.⁵ My belief that it's going to rain contributes to the satisfaction of various desires of mine (the desire that my laundry not get wet, which interacts with the belief and causes me to put my laundry in the dryer rather than hanging it on the clothesline; the desire not to get rained on myself, which interacts with the belief and causes me to take an umbrella with me when I go out) only if it does actually rain. If it does not rain, I and my laundry will

³ Thanks to an anonymous referee for the objection, for suggesting a minimal condition similar to this one, and for one of the examples below of non-proper-functional but useful traits.

⁴ A *Normal explanation* is an explanation of how, historically, a type of thing has performed its proper function. Where R is a type of object and F is the function of objects of that type, [the most proximate Normal] explanation is the *least detailed* explanation possible that starts by noting some features of the structure of members of R, adds some conditions in which R has historically been when it actually performed F—these conditions being uniform over as large a number of historical cases as possible—adds natural laws, and deduces, i.e. shows in detail without gaps, how the setup leads to the performance of F. (Millikan, 1984, p. 33) The *Normal conditions* for the performance of a mechanism's proper function are the conditions that must be mentioned in the most proximate Normal explanation of the proper functioning of that mechanism.

⁵ Note that Normal conditions are Normal conditions for the performance of a particular proper function—if an item has multiple proper functions, these functions may not have the same Normal conditions. Note also that Normal conditions are not *necessary* conditions: there may be cases in which my belief that there is coffee at Stacey's helps me to satisfy my desire for coffee even if there is no coffee at Stacey's, if, for example, there is a coffee shortage and Stacey has run out, but he directs me to the nearest cafe that still has some.

stay dry, but my belief that it's going to rain will not have played any role in making it so. The imminence of rain is a Normal condition for the performance of the proper function of my belief that it's going to rain.

Suppose, now, that there are ways that the belief that it is going to rain has historically contributed to fitness *other* than by participating in inferences that lead to the satisfaction of desires, or more generally, that there are ways that our belief-forming mechanisms have contributed to fitness other than by generating beliefs that do this. This will not undermine Millikan's teleosemantics, because that theory appeals to the Normal conditions for the performance of this particular function of beliefs. No claim is made that this is the only proper function of beliefs. What would undermine teleosemantics would be an argument that participating in inferences that lead to the satisfaction of desires is *not* a proper function of beliefs—but that is not a consequence of accepting a proliferation of proper functions.

Only one function of beliefs is, on Millikan's view, relevant to the determination of their content: the function of participating in inferences that lead to the satisfaction of desires. Adding more functions does not undermine the claim that this is *one* of the functions of beliefs, or the plausibility of the claim that this is the content-determining function. Thus the suggestion at hand, that a trait may have more proper functions than we normally think, need not be a problem for Millikan's teleosemantics.

5 The challenge of Christie, Brusse, Bourrat, Takacs and Griffiths

Christie et al. do not cast their challenge to the selected effects account in terms of degrees of natural selection, but like Matthewson, they think that the selected effects account does not pay sufficient attention to the details of how natural selection actually operates.

They begin by constructing what they describe as a canonical version of the selected effects account.

Consider a population of organisms some of whom have character state C_i . These organisms are descendants of organisms with C_i , and their character states are homologous. In this population, C_i has effect F as a Proper function if and only if:

- (1) In some ancestral populations there was variation in C .
- (2) Having state C_i caused some ancestral individuals to produce effect F with higher probability than individuals with alternative character states.
- (3) Performing F caused some ancestral individuals with C_i to have greater reproductive output than they would have had if C_i had been changed to an alternative character state extant in that ancestral population (C_j).
- (4) The frequency of C_i in the current population is influenced by selection for C_i in these ancestral populations in virtue of the increase in fitness accruing to individuals with C_i from performing F more frequently than individuals with alternative character states. (Christie et al. forthcoming, pp. 8, 9)

The main difference between this canonical account and the selected effects accounts of Millikan and Neander is that the canonical account takes as its explanans

the frequency of a trait in a current population, rather than the possession of the trait by a particular current individual. This shift is not accidental. Christie et al. say that “the actual evolutionary explanations that biology produces explain facts about populations” (p. 8), and thus they “depart from Millikan’s formulation by defining Proper function for the members of a population, not for a specific individual” (p. 8). “Canonical” is perhaps not the right label. This is supposed to be an *improved* selected effects account: improved by being made more consistent with the explanatory practices of evolutionary biology. Where Millikan and Neander attribute functions to traits of individuals (such as the blue head of Walter the fairy wren), Christie et al.’s canonical selected effects account attributes functions not “to Walter’s blue head in particular, but blue heads in the population of which Walter is a member... [Evolutionary explanations explain] the proportion of a trait in a population, not why it ‘exists’.” (Christie et al., p. 8).

However, there can be an explanation of the presence of a particular trait in a particular individual that is at least in part an evolutionary explanation. It will be a more detailed explanation than evolutionary biologists normally deal in—it will look at the particular lineage that Walter belongs to, and what blue heads have done, if anything, for the individuals in that lineage.⁶ I will argue that some of the problems that Christie et al. identify with their canonical account result from features that they themselves have introduced, and that it is not clear that they are problems for the Millikan/Neander version of the selected effects account.

Selected effects theorists, Christie et al. say, “use simple, intuitive examples of natural selection presented via verbal scenarios. These scenarios assume a uniform selective environment. But when that assumption is dropped, then it is not generally true that selected effects functions explain the traits that bear them.” (p. 3). In cases where the environment is not uniform, Christie et al. claim, the explanation generated by the selected effects account of proper function does not match the actual evolutionary explanation of how the trait came to be the way it is. The selected effects theory focuses on the occasions on which a trait has been successful, and those may constitute a very small part of the evolutionary history of the trait. Christie et al. issue a challenge:

We hope that selected effects theorists will take this on board and dig into the evolutionary details to see if their program can really be carried out. Until this work is done, the SET [selected effects theory] runs the risk of merely hand-waving at natural selection to lend an air of respectability to normative intuitions (p. 5).

Matthewson’s peppered moth example is a case of the kind Christie et al. are talking about: a case in which the selective environment has not been uniform, and consequently there has not been a consistent history of selection for one form of a trait. Christie et al. give a number of other examples. Co-evolution cases are one kind of example: they consider a hypothetical case in which a zebra’s striped coat is initially favoured because flies are less likely to bite it than plain coats, but as

⁶ See also the Elliot Sober/Karen Neander debate about what natural selection explains, including Neander (1995b, c); Sober (1995), see Walsh (1998) for an overview.

striped coats come to predominate in the population, fly preferences evolve so that striped coats are more likely to be bitten than plain ones—so, as with the peppered moth case, the direction of selection, in this case for and against stripes, changes over time. The stripes case is also a case of frequency-dependent selection (a trait increases fitness when it is rare in a population but decreases fitness once it reaches a certain level in the population): these are always going to be cases in which the selective environment is not uniform, as one component of the selective environment is the other members of the population. Christie et al. also provide a more detailed real-life case of frequency-dependent selection: it concerns two character states of the Gouldian finch, black-headedness and red-headedness, which are in equilibrium in the population. Finally, Christie et al. give an example of an evolved “bet-hedging” strategy; a plant producing seeds that do not all germinate in the following year, so that if there is a bad year (for example, a drought) some seeds will survive to germinate in a better year. All of these cases are ones in which the selective environment is not uniform. Christie et al. think that the selected effects account assumes a uniform selective environment, and that its teleological explanations of the presence of traits will not line up with the actual evolutionary explanation for any trait that has evolved in a heterogeneous selective environment.

I will discuss the peppered moth case and the bet-hedging example,⁷ and then briefly consider the Gouldian finch as an example of frequency-dependent selection.

In the peppered moth case, there are two different colorations present in the moth population, darker and lighter. The standard story (it turns out not to be perfectly accurate, but it serves as a useful illustration anyway⁸) is that light-coloured moths were harder for predatory birds to see in the forests of pre-industrial England, as the tree trunks were also light in colour. However, the airborne soot of the industrial revolution darkened the tree trunks, and so dark coloration became fitness-enhancing, and dark-coloured moths proliferated. Later, however, with cleaner technologies, the forests became lighter again, and light coloration was again fitness-enhancing.

Matthewson says about this case that if we try to retain a binary view of biological functions,

... it seems we would be committed to saying one of three things: that both light and dark coloration have functions (not being seen against light or dark backgrounds respectively) in just the same way and to the same extent; that neither has a function; or that one has a function but the other does not. None of these options articulates what really seems to be going on in this example—that light and dark pigmentation both have functions right now, but not in precisely the same way. One of these functions is currently on the wane, as its selective fortunes have been reversed. (12)

Christie et al. point out, about similar cases in which the environment in which selection has taken place has not been uniform, that the selected effects account focuses exclusively on those periods in the selectional history during which a trait has been

⁷ See also Kingsbury (forthcoming).

⁸ See Cook (2013) for an overview of the literature on the peppered moth and industrial melanism stretching back to (White, 1877).

fitness-enhancing. They think that consequently the selected-effects explanation of the presence of a trait does not coincide with the actual evolutionary explanation, which includes also the periods during which the trait was fitness-reducing.

What *does* the selected effects account have to say about the peppered moth case? The selected effects theorist starts with a present-day trait and gives an account of how that trait has contributed to ancestral fitness, thus explaining the presence of that trait now. There are two traits to be considered in this case: dark coloration and light coloration. First consider the trait of dark coloration in peppered moths. What that trait has contributed to ancestral fitness is that (during periods when the tree trunks were dark-coloured) it has helped moths to avoid being eaten by predators. This (partially) explains why there are now dark-coloured moths. Now consider the trait of light coloration in moths. What this trait has contributed to ancestral fitness is that (during periods when the surrounding tree trunks were light-coloured) it has helped moths to avoid being eaten by predators. This (partially) explains why there are now light-coloured moths. Both traits have the function of camouflage, but in the periods during which light coloration succeeded in performing that function, dark coloration did not, and vice versa. That is to say, the selected effects theorist chooses the first of Matthewson's three options: "both light and dark coloration have functions (not being seen against light or dark backgrounds respectively) in just the same way and to the same extent". However, to *have* a function is a different thing from *performing* that function. If the forests are currently light, then the dark coloration of a dark moth is not currently in an environment in which it can perform its function.⁹ The fact that dark coloration is not currently performing its function does not mean that it does not have that function, nor that it has it in a different way or to a different extent from a trait, in this case light coloration, that can in its current environment perform its function.¹⁰

It is true, as Christie et al. point out, that the selected effects account focuses on those periods of the evolutionary history of a trait when the trait has been fitness-enhancing. Is it also true that because of this, the selected effects explanation comes apart from the actual evolutionary explanation of the light coloration of a present-day moth? A complete evolutionary explanation of the light coloration of a present-day moth would include not just what happened during those periods when light coloration was fitness-enhancing, but also how it came about that the ancestors of the present light-coloured moth survived those periods when light coloration was fitness-reducing. That means that the selected effects explanation, focusing on the periods when light coloration contributed to fitness, is a partial explanation. However, the selected effects explanation is not *false*, and no assumption is made by the selected effects theorist that light coloration has always been fitness-enhancing. It is just that when you are starting from the assumption that light coloration has a proper function, and asking what that function is—"What is light coloration for?"—it makes sense to focus on those occasions when light coloration has been useful. It would be odd, in this context, to

⁹ Sterelny and Griffiths (1999) draw the distinction between something's being an adaptation—something that has been naturally selected for—and it's being currently adaptive—fitness-enhancing in its current environment.

¹⁰ An alternative would be to move to something like the "modern history" approach suggested in Godfrey-Smith (1994), but I think I have shown that this move is not necessitated by examples in which the direction of selection changes across time.

include in your explanation those periods when light coloration has tended to *decrease* the likelihood that a moth would survive.

Note that I am assuming that the thing to be explained is a characteristic of a present-day individual. If that is the thing to be explained, then the peppered moth case and others like it do not appear to pose a problem for a selected effects account. If, as in Christie et al.'s canonical account, the thing to be explained is the frequency of a characteristic in a present-day population, then we may need the more detailed account of how the environment has changed and the fortunes of the competing traits have consequently ebbed and flowed—but changing the question and then objecting to selected effects theorists failure to answer a question they were not trying to answer is surely not a legitimate argumentative move.

Now for the bet-hedging example. If all of a plant's seeds germinate every year, the plant will be very successful in a year in which the conditions for germination and seedling establishment are good, but very unsuccessful in a drought year. Some annual plants evolve a diversified strategy, producing seeds that germinate in different years. These *bet-hedging* plants do less well in a good year than plants whose seeds all germinate every year, but a population of them will persist across a drought year in which a population of the other type will die out. The present-day trait of producing seeds that germinate across several years has presumably evolved precisely because conditions during the season when seeds germinate and seedlings get established have varied from year to year.

What the selected effects theory has to say about this depends on what trait we focus on. Christie et al. say "In this example, we believe that Millikan would apply the idea of Normal explanation to individual seeds" (p. 18) and the function of germination - and that is clearly one possible focal trait. The function of an individual seed is to germinate: that's what seeds are for. Normal conditions for the performance of this function are the presence of sufficient warmth and moisture in the spring: if these conditions don't hold, then the seed does not germinate. That an individual seed has not performed its proper function until it has germinated seems right, on the face of it.

But the more interesting present-day trait is the production of seeds that don't all germinate in the same year—the bet-hedging strategy itself—and there is no problem with giving a selected effects account of its presence in a particular plant. What has the trait contributed to fitness? It has enabled the plant's ancestors to continue to reproduce despite variable conditions. It is surely plausible that this is what the bet-hedging strategy is for, and that normal conditions for the performance of this function are that levels of moisture and warmth in the spring are variable from year to year. (Under consistent drought conditions, the production of seeds that germinate across several years will not enable the plant to reproduce. Under consistently favourable conditions, the plant will reproduce, but not as successfully as one that produces seeds all of which germinate in the following spring.)

What explains a particular plant's production of seeds that do not all germinate in the same year is that some of its ancestors encountered variable conditions that meant that this trait contributed to fitness. As before, this is not a complete explanation of why the trait is present, but the contribution to fitness of the bet-hedging strategy is surely a salient part of that explanation, if your interest is in the proper function of the present-day trait of producing seeds that do not all germinate in the same year.

The upshot of this discussion of the peppered moth case and the bet-hedging case is that it is not obvious that the selected effects theorist *does* need to “dig into the evolutionary details” in order to find a way to give a firm grounding to their theory and avoid the charge of “merely hand-waving at natural selection to lend an air of respectability to normative intuitions”. Rather, selected effects theorists and their critics need to clearly state what it is that is being explained, and the selected effects theorist needs to acknowledge that their explanation of the presence of present-day traits in terms of past contributions to fitness is only a *partial* explanation of the presence of the present-day trait.¹¹

Finally, let’s consider frequency-dependent selection and the Gouldian finch (Christie et al., forthcoming), pp. 12–15. Black-headed Gouldian finches produce high levels of testosterone and corticosteroids which cause them to aggressively compete for nesting cavities; red-headed Gouldian finches do not, investing their resources in parenting rather than conquest, and raising more successful broods. There is some mating between red and black-headed finches, but not much, and hybrid offspring have reduced fitness. The two types persist in wild populations at a ratio of approximately three black to one red. If the proportion of reds rises, the aggressive strategy becomes more costly, as the odds of getting into a fight over a nesting cavity with a fellow-red increases.

Christie et al. think that cases like this are a problem for the selected effects account.

The fact that Elevated [testosterone and corticosteroids] has the selected effects function < defeating rivals for nesting cavities > is supposed to answer the question, “what explains the frequency of Elevated in the current population?” The actual evolutionary explanation is that selection is frequency dependent and takes the population to an equilibrium frequency where the fitness of the two types is equal. The selected effect function explanation discards this information and includes only information about why Elevated was sometimes fitter than Reduced.... The fact that Elevated is sometimes fitter than Reduced does not explain why the frequency of Elevated is 25% or even why Elevated coexist with Reduced at any frequency, rather than being fixed.

Note, however, that if the selected effects theorist is trying to explain the elevated testosterone and corticosteroids of a particular present-day finch, rather than the frequency of Elevated in the current population, this objection does not get off the ground. The explanation of why a particular finch has Elevated is, at least in part, that its ancestors having Elevated enabled them to win battles for nesting cavities and thus reproduce successfully. The objection works against the so-called canonical selected effects account, but not against the selected effects accounts of Millikan and Neander which attribute traits to functions of individuals. My discussion here brings out the importance of being clear, in all cases, about exactly what it is that a particular evolutionary explanation is an explanation *of*.

¹¹ Garson (forthcoming) suggests that selected effects theorists have acknowledged this all along.

6 Conclusion

Both Matthewson and Christie et al. challenge selected effects theorists to resolve apparent discrepancies between the selected effects account and the details of how natural selection actually works.

Matthewson suggests that natural selection comes in degrees, and argues that the selected effects theorist needs to either accept that proper functionhood also comes in degrees, or find a principled cut-off point, distinguishing selection that does confer proper functions from selection that is too weak to do so. Here I have explored the suggestion that *any* degree of natural selection suffices to confer proper functions, and in particular the consequences of this view for teleosemantics, concluding that Millikan's teleosemantics at least is not undermined by it.

Christie et al. provide examples of situations in which (they claim) the actual evolutionary explanation of a trait comes apart from the selected effects explanation. I have argued that their examples do not succeed in undermining the selected effects account. The selected effects theorist does not need to revise or abandon their account of proper function, but only to keep a clear focus in each case on exactly what present-day trait is their explanatory target and to make it clear that, like any other causal explanation, their teleological explanations are partial explanations.

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Declarations

Conflict of interest Author declare that they have no conflict of interest to disclose.

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