Chapter 8: A non-causal account of design explanation

8.1 Introduction

Let us take stock. As I explained in chapter 1, I aim to understand a certain practice in functional biology. Functional biology is that part of biology which is concerned with the life of individual organisms: the way they are built, the way they work and the way they behave. As I have shown by many examples, functional biologists often explain why an organism is built the way it is built, why it works the way it works, or why it behaves the way it does, by appeal to the causal roles of the items and behaviours in the maintenance of the organism and the survival value of the character those items and behaviours have. I aim to understand what this activity adds to our knowledge. This activity is usually called ‘functional explanation’ by those who engage in it. I use the term ‘design explanation’ to avoid confusion with other uses of the term ‘functional explanation’.

In chapter 5 I argued that Cummins gives a satisfactory account of the meaning of the notion of function as causal role, but not of the use of attributions of function as causal role in design and evolutionary explanations. In chapter 2 and in chapter 5 I distinguished the notion of function as causal role from the notion of function as survival value and I presented and defended a new account of the latter notion.

In chapter 4–7 I discussed the different accounts of functional explanation presented by philosophers. I argued that those philosophers are (in part) concerned with different kinds of explanations. There are at least three different kinds of explanations which are called functional explanations (at least by some philosophers):

1) functional explanation$_{1:}$ functional analyses in Cummins’s sense (capacity explanations)
2) functional explanation$_2$: the kind of explanations in which I am interested (design explanations),
3) functional explanation$_3$: functional explanations in the sense of the etiological theory, (selection explanations).

I argued that the different accounts of functional explanation presented by philosophers up to now fail to give a satisfactory account of design explanations.

In this chapter I detail my own account. The basic idea of my account is that design explanations relate the way an organism is built, the activities of its parts, its behaviour and the condition of the environment in which it lives in terms of what is needed or useful to survive and reproduce rather than in terms of causes. In section 8.2 I describe the structure of design explanations. I argued that design explanations typically start with an attribution of a causal role and then proceed in one of the following two ways. If they address a type (4a) question (why is it useful to have a certain item or perform a certain behaviour?) they continue by explaining why it is useful to perform that causal role by pointing to the demands imposed on the organism in the conditions that apply to the organisms in study. If they answer a type (4b) (why does a certain item or behaviour has the character it has?) they continue by explaining why it is useful to perform that causal role in the way in which it is performed by pointing to the demands upon that causal role in the conditions in which the organisms in study live. In the next two sections I am concerned with the subject of design explanations. In section 8.3 I discuss the different kind of relations that are the subject of the different kinds of explanation in functional biology. I contend that explanations show us how a certain phenomenon fits into the structure of the world and I argue that there are three kinds of fundamental relations in the organic world: causal relations at the individual level, causal relations at the population level and functional interdependencies at the individual level. In section 8.4, I answer the question what design explanations add to our knowledge. My answer is to that question basically this: design shows us how the trait to be explained fits into the structure of functional interdependencies of a living organisms.

8.2 The structure of design explanation

8.2.1 The core of a design explanation

Design explanations are answers to a question of the following form:

‘why do s-organisms have / perform t_1 rather than t_2, t_3, … t_n?’.

In which:

s	a set of organisms[1] (the phrase ‘s-organisms’ refers to the members of that set)
t_1	a trait (i.e. the presence or character of a certain item or behaviour) of s-organisms
t_2, t_3, … t_n	traits which s-organisms lack

I shall call the set {t_1, t_2, t_3, … t_n} the ‘reference class’.[2] Trait t_1 will be called ‘the trait in question’, t_2, t_3, … t_n will be called ‘the alternative traits’.

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[1] Note that s does not necessarily consists of organisms of one taxon. The set might be taxonomically heterogeneous. That is, it may lump together organisms that belong to more than one taxonomic group (e.g. fishes) and/or it may excluded certain members of a certain group (e.g. green plants, land mammals).

[2] Note that my notion of reference class is akin to but different from Van Fraassen’s (1980) notion of ‘contrast class’. The contrast class in Van Fraassen’s sense would be: {‘s-organisms have / perform t_1’, ‘s-organisms have / perform t_2’, ‘s-organisms have / perform t_3’, ..., ‘s-organisms have /perform t_n’}. The reason why I use my

In the preceding sections I have discussed many examples of such questions. Among others:

- why do snakes have a forked tongue rather than a blunt one?
- why do "larger" organisms have rather than lack a circulatory system?
- why do fishes respire by means of gills rather than by means of lungs?
- why do mountain gazelles mark their territories by dung piles rather than by scent marks?
- why do birds remove the empty egg shell after the chick has hatched rather than leave it where it is?

However, not every why-question of this form counts as a request for a design explanation. Why-questions in biology are notoriously ambiguous. In section 2.3.2 I distinguished three types of why-questions:

1) questions that ask for causes at the level of an individual organism, such as the mechanisms that bring about a snakes forked tongue or the signals that release the egg shell removal behaviour in birds (why$_1$-questions),
2) questions that ask for the utility of a trait, such as the utility of a forked tongue or the utility of the egg shell removal behaviour (why$_2$-questions),
3) questions that ask for evolutionary causes, such as the mechanisms that brought about the forked tongue or the egg shell removal behaviour in the course of the evolution (why$_3$-questions).

Design explanations are answers to why$_2$-questions. So the general form of a request for a design explanation is:

'why$_2$ do *s*-organisms have / perform t_1 rather than t_2, t_3, … t_n?'.

The core of an answer to a why$_2$-question consists of two statements of the following form:

(1) *s*-organisms live in condition c_u.

(2) in condition c_u trait t_1 is more useful than trait t_2, t_3, … t_n.

In which:

c_u a conjunction of one or more conditions of organisms and/or the environment in which they live[3]

For example, the core of the answer to the question 'why$_2$ do fishes respire by means of gills rather than by means of lungs?' consists of the following statements:

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own notion rather that Van Fraassen's is that I want to say such things as 'the trait in question is the best one in the reference class'.

[3] The subscript *u* is added to the *c* of 'condition' to emphasize that *c* refers to the conditions in which a certain trait is useful not to the conditions that bring about (cause) that trait.

(1) Fishes typically live in water.

(2) In water it is more useful to respire by means of gills than by means of lungs.

I will represent the train of thought of design explanations (functional explanations$_2$) in the following form:

(1) s-organisms live in condition c_u.

(2) in condition c_u trait t_1 is more useful than trait t_2, t_3, … t_n.

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(3) that's why$_2$ s-organisms have / perform t_1 rather than t_2, t_3, … t_n.

For example:

(1) Fishes typically live in water.

(2) In water it is more useful to respire by means of gills than by means of lungs.

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(3) That's why$_2$ fishes respire by means of gills rather than by means of lungs.

The final statement in this series indicates (i) what question is addressed by the explanation, and (ii) that at this point of the reasoning that question is supposed to be sufficiently answered. It is worth emphasizing that this train of thought is not an argument in the logical sense of 'argument': it does not consist of a series of premises that support a conclusion. It is not required that the part after 'that's why' in the final statement follows logically from the premises. In order to be a good explanation it is required that

- the explaining statements are well supported,
- any other requirements concerning the scientific status of the explaining statements are met,
- the statements in the scheme are related in the way indicated by the symbols in the scheme,
- any other requirements concerning the (inferential) relation between the different statements in the scheme are met,
- the symbols in the scheme are filled in in accordance with the filling instructions.

The first statement in this train of thought is an empirical generalization. The second is an attribution of survival value, which is a lawlike statement. As I will explain in section 8.3.4, this statement states that condition c_u is a non-redundant part of a condition that is sufficient for the utility of t_1 over t_2, t_3, … t_n. In such cases it is said that c_u imposes a demand for t_1 on the relevant item or organism or that c_u demands for t_1. For example, living in water imposes a demand for gills on fishes and using the tongue in chemical tropotaxis imposes a demand for being forked on the snakes tongue. Usually t_1, t_2, t_3, … t_n can be viewed as different states of the same character or different determinations of the same determinable property.

There are several ways in which an item or behaviour can be useful. Roughly speaking, three criteria for usefulness can be distinguished: (1) the efficiency with which a certain task is performed, (2) the effects on survival, and (3) reproductive success. The first criterion is, for example, used in Schwenk's explanation of the snake's forked tongue. Schwenk observes that a forked tongue is more useful than a blunt one because a blunt one would be of no use in the mechanism of chemical tropotaxis. The second criterion is used in the explanation of why fishes have gills rather than lungs. This explanation points out that organisms that live in water are less viable if they have lungs than if they have gills. Similarly the explanation of why e.g. Vertebrates transport oxygen by means of a circulatory system points out that organisms that are larger than a certain size are more viable if they transport oxygen than if they rely on diffusion alone. The third criterion is employed in Tinbergen's explanation of the egg shell removal behaviour. Tinbergen points out that birds that are predated by carrion crows and herring gulls have more reproductive success if they remove the empty egg shell than if they leave it near the nest.

As I showed in the preceding chapters, philosophers have different opinions about what the hallmark is of functional explanation. Most of the classical authors characterize functional explanations (usually they called them 'teleological explanations') as explanations that appeal to effects rather than to causes. Cummins (1975, 1983) has defended the view that functional explanation (he calls them 'functional analyses') are characterized by the fact that they appeal to causal roles in maintaining a certain capacity. On the etiological view the hallmark of functional explanations is their teleological nature, that is the alleged fact that they appeal to what a certain item evolved for.

In my view the analyses of those other philosophers apply in part to different kinds of explanations (different from each other and from the kind of explanations that are central to this thesis). Cummins's analysis applies to capacity explanations. In chapter 7 I have raised doubts the kind of explanations envisaged by the teleological theory, but anyway such explanations are different in kind from both capacity explanation and design explanations. The hallmark of design explanations is their appeal to utilities. As utilities are usually assessed in relation to causal roles (function$_2$), design explanations typically start with a function$_2$ attribution (attribution of a causal role) but it is the appeal to utilities and not the appeal to causal roles that gives design explanations (functional explanations$_2$) their special status and what makes them different from causal explanations.

8.2.2 Appeal to causal roles

In the previous section I emphasized that the hallmark of design explanations (functional explanations$_{2)}$ is their concern with the utility of a certain trait. Nevertheless attributions of causal role (function$_2$ attributions) play an important role in design explanations. This is because utilities are usually assessed in relation to causal roles. The role of attributions of causal roles in design explanations is the subject of this section.

Roughly speaking, two types of design explanations (functional explanations$_2$) might be distinguished (see section 2.3.2, and the examples of section 6.2): design explanations that answer a type (4a) question (why is it useful to perform a certain causal role?) and design explanations that answer a type (4b) question (why is it useful that a certain item or behaviour has a certain character?). Explanations of both types typically start with an attribution of a causal role *f* (say respiration) to an item or behavioural pattern *i* (such as the gills of fishes). From there they proceed in different ways. The first type of design explanation is concerned with the survival value of the attributed causal role. It addresses the question ‘why$_2$ do s-organisms have an item / behaviour that performs task *f*?’ (e.g. ‘why$_2$ do fishes have a respiratory system?’). The second type of design explanation is concerned with the specific way in which the attributed causal role is performed. It addresses the question ‘why$_2$ is task *f* performed in the way it is performed rather than in some other way’ (e.g. ‘why$_2$ do fishes respire by means of gills rather than lungs?’).

An example of a design explanation of the first type (which answers a type 4a question) is Krogh’s (1941) explanation of the need for a system that transports oxygen, discussed in section 4.2.3. This explanation can be reconstructed as follows:[4]

(1) The distance between the inner organs and the periphery of vertebrates is more than 1 mm.
(2) If the distance between the inner organs and the periphery of an organism is more than 1 mm it is useful to that organism to transport oxygen.
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(3) That’s why$_2$ vertebrates have a system that transports oxygen.

More generally, the core of a design explanation (functional explanation$_2$) which explain why an organism has an item that performs a certain task has the following scheme:

(1) s-organisms live in condition c_u.
(2) In condition c_u it is useful to perform *f*.
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(3) That’s why$_2$ s-organisms have an item / behaviour that performs *f*.

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[4] This a *very* rough sketch of Krogh’s explanation. Recall that Krogh’s main achievement was the application of Fick’s law of diffusion to the problem of circulation and respiration. This law is not even mentioned in this rough sketch. This is because this section is concerned with the role of attributions of causal roles in survival value explanations. The explanatory role of physical laws is discussed in section 8.2.3. In this section I give a more detailed sketch of Krogh’s explanation.

In which:

f a causal role (function_2).[5]

The first statement in this scheme is an empirical generalization about the conditions in which the organisms live to which the explanation applies. The second statement is an attribution of survival value. The phrase 'in condition c_u it is useful to perform f' should be read as 'in condition c_u it is more useful to be able to perform f than to live without that capacity'. This is a lawlike statement.

An explanation with this kind of core is often given in answer to a question of the following type:

why_2 do *s*-organisms have item / behaviour *i*?

The answer to this question has the following structure:

(1) *s*-organisms live in condition c_u.

(2) in condition c_u it is useful to perform *f*.

(3) in *s*-organisms item / behaviour *i* contributes to task *f*.

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(4) That's why_2 *s*-organisms have / perform *i*.

In which:

i a certain type of item or behaviour[6] (the phrase 'item / behaviour *i*' refers to items or behaviours of type *i*).

For example:

(1) The distance between the inner organs and the periphery of vertebrates is more than 1 mm.

(2) If the distance between the inner organs and the periphery of an organism is more than 1 mm it is useful to that organism to transport oxygen.

(3) In vertebrates the circulatory system transports oxygen.

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(4) That's why_2 vertebrates have a circulatory system.

The first statement in this scheme is an empirical generalization about the conditions in which the organisms to which the explanation applies live. The second statement (an appeal to survival value) is a lawlike statement saying that in the conditions stated in the first statement it is useful to perform a certain task (function_2). The third statement (an attribution of a causal role

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[5] As I discussed in section 5.1 I agree with Cummins (1975) that functions_2 (causal roles) are singled out by their role in capacity explanations.

[6] Recall that items are grouped together on the basis of homology (chapter 7). If items / behaviours were identified in terms of their role the first statement in this scheme would be tautologous.

(function$_2$)) is an empirical generalization about how that task is performed in the organisms to which the explanation applies. It says that in those organisms that causal role is performed by the item or behaviour to be explained.

This first kind of design explanation is concerned with the need to perform a certain causal role, it says nothing about the character of the item or behaviour that performs that causal role. The second kind of design explanation is concerned with the way in which a certain causal role is performed and, therefore, with the character of the item or behaviour that performs the causal role. The core of this second type of design explanation (which answers a type 4b question) has the following structure:

(1) *s*-organisms live in condition c_u.

(2) In condition c_u it is more useful to perform *f* by means of an item / behaviour that has character s_1 than by means of an item / behaviour that has character s_2.

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(3) that's why *s*-organisms perform *f* by means of an item / behaviour that has character s_1 rather than by means of an item / behaviour that has character s_2.

In which:

s_1 a description of *i*'s form or activity (function$_1$),

s_2 a description of a form or activity that does not apply to *i*.

An example is the explanation of why fishes respire by means of gills rather than lungs given in section 6.2.2. This explanation can be summarized as follows:[7]

(1) Fishes live in water.

(2) In water it is more useful to respire by means of invaginated structures (gills) than by means of evaginated structures (lungs).

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(3) That's why$_2$ fishes use invaginated structures (gills) rather than evaginated ones (lungs) to respire.

Another example is the explanation of Habibi c.s. (1993) of why mountain gazelle's mark their territories by dung piles rather than by scent marks (example 3.3. of section 2.2.3). This explanation can be reconstructed as follows:[8]

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[7] Just as in the scheme of Krogh's presentation this is a very rough sketch. I have left out the elaboration on why gills are more useful than lungs. This part of the explanation is discussed in section 8.2.3

[8] This is, once again, a very rough sketch. I have left out Habibi c.s. explanation of why it is the case that in large territories it is more useful to mark territories by means of dung piles rather than scent marks. This part of the explanation is discussed in section 8.2.3.

(1) Mountain gazelle’s have large territories.

(2) In case of large territories it is more useful to mark territories by means of dung piles than by means of scent marks.

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(3) That’s why$_2$ mountain gazelle’s mark their territories by dung piles rather than by scent marks.

In morphology, this kind of explanation is often brought up in answer to a question of the following form:

why$_2$ does item i of s-organisms has character s_1 rather than s_2?

The answer to such a question has the following structure:

(1) In s-organisms: item i performs causal role f

(2) s-organisms live in condition c_u

(3) In condition c_u it is more useful to perform f by means of an i that has character s_1 than by means of an i that has character s_2.

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(4) That’s why$_2$ in s-organisms item i has structure s_1 rather than s_2

A clear example is Schwenk’s (1994) explanation of why snakes have a forked tongue (example 2.3 of section 2.2.2):

(1) The tongue of snakes has a causal role in trail following

(2) Snakes follow trails by comparing chemical stimuli simultaneously sampled at two sides

(3) In order to sample chemical stimuli simultaneously at two sides it is more useful to have a forked tongue than a blunt one

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(4) That’s why snakes have a forked tongue rather than a blunt one.

The favourite explanation of many philosophers also follows this scheme:

(1) The function$_2$ (causal role) of hearts of vertebrates is to propagate the blood.

(3) In order to propagate the blood it is more useful if the heart beats than if it stands still.

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(4) That’s why the heart of vertebrates beats.

Note that in this example (just as in the others) the function$_2$ attribution (attribution of a causal role) is a first step in the explanation, not the complete explanation. This in contrast to popular beliefs.

In ethology the second kind of explanation is often invoked to answer a question of the following form

why$_2$ do s-organisms perform behaviour s_1 rather than s_2?

in which:

s_1 describes a behaviour s-organisms perform,

s_2 describes a behaviour s-organisms do not perform.

The answer to such a question has the following form:

(1) In s-organisms: behaviour s_1 performs causal role f.

(2) s-organisms live in condition c_u.

(3) In condition c_u it is more useful to perform f by means of a behaviour that has character s_1 than by means of a behaviour that has character s_2.

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(4) That's why$_2$ s-organisms perform s_1 rather than s_2.

In this section I have shown that function attributions have two important explanatory roles in design explanations (functional explanations$_2$). Utilities are usually assessed in relation to functions$_2$ (causal roles). For that reason, design explanations typically contain a statement which says that it is more useful to perform a certain causal role (function$_2$) in the way it is performed than in some other way. Furthermore, because utilities are usually assessed in relation to functions$_2$ (causal roles) it is a good strategy to start to look for a function$_2$ (causal role) of an item or behaviour if you want to explain the presence or the specific character of that item or behaviour by means of a design explanation. Hence, design explanations of the presence or the character of an item or behaviour typically start with a function$_2$ attribution (attribution of a causal role). They then proceed to show that it is more useful to perform that function by an item or behaviour with the character which that item or behaviour actually has than by an item or behaviour with some other character. Function$_2$ attributions (attributions of a causal role) are the first part of such explanations, but not the complete explanation.

8.2.3 Optimality claims and requirement claims

In section 8.2.1 I stated that the core of a design explanation consists of two claims. One states that in certain conditions the traits to be explained are more useful to the organisms that have them than some other traits which they have not. The other claims that those conditions apply to the organisms concerned. In section 8.2.2 I added that utilities are usually assessed in relation to functions$_2$ (causal roles). The utility claim, therefore, usually takes the form of a claim about the utility of performing a certain function$_2$ (causal role) in a certain way. Claims about utilities may vary in strength. I distinguish two types: optimality claims and requirement claims. Optimality claims claim that the trait in question is the best one in the reference class. They have the following form:

in condition c_u trait t_1 is more useful than each of the following traits: t_2, t_3, … t_n

For example: ‘if the tongue is used in trail following by means of chemosensory tropotaxis a more deeply forked tongue is more useful than a less deeply forked tongue’. The ultimate criterion for utility in optimality claims is inclusive fitness. That is, ultimately it is claimed that the inclusive fitness of the organisms in question is higher if they have trait t_1 than if they have one of the other traits in the reference class instead of t_1. However, as utility is usually assessed in relation to function$_2$ (causal role) one often finds claims to the effect that the trait in question performs a certain function$_2$ more efficiently than any other trait in the reference class (for example ‘a more deeply forked tongue is more efficient in performing chemosensory tropotaxis than a less deeply forked one’). In such cases it is tacitly assumed that efficient performance results in greater fitness.

Requirement claims claim that the trait in question is the only one in the reference class that works. They have the following form:

> in condition c_u trait t_1 is the only one that is useful among the following traits: t_1, t_2, t_3, … t_n

For example: ‘if an organism lives on land, lungs are useful but gills not’. I discuss the precise meaning of requirement claims and related notions in section 8.4. Depending on the criterion for utility one may distinguish between viability claims and functionality claims. Viability claims claim that the trait in question is the only one in the reference class that enables the organism to survive and reproduce. Functionality claims claim that the trait in question is the only one in the reference class that enables the organism to perform a certain function$_2$ (causal role). The distinction between viability claims and functionality claims is a gradual one. The above claim about the utility of lungs is clearly a viability claim because it implies that land organisms that respire by means of gills are not viable (cannot get enough oxygen to survive and reproduce). Since biologists are usually interested in the survival value of a certain trait, real examples of pure functionality claims are rare. Schwenk’s claim that a forked tongue is useful in chemosensory tropotaxis but a blunt one not has for example both functionality and viability aspects. It is formulated as a claim about what is required to perform a causal role, but it has implications about survival: Schwenk points out that the ability to perform chemosensory tropotaxis is important in finding preys and mates.

If the reference class is in a certain sense complete (e.g. because the reference class contains all possible states of a certain character or because the presence of a certain item is compared to its absence) one says that the trait in question is *needed* (in order) to survive and reproduce or (in order) to perform a certain function. For example, Krogh claimed that larger organisms need a system of convection in addition to diffusion. The explanation of why fishes have gills rather than lungs points out that fishes need gills (rather than lungs) to survive and reproduce. Schwenk points out that snakes need a forked tong to perform chemosensory tropotaxis.

Simple design explanations might be classified either as optimality explanations or as requirement explanations depending on whether the utility claim is a optimality claim or a requirement claim. However, many design explanations are complex in the sense that they contain more than one utility claim and in that case they might contain both optimality claims and requirement claims.

8.2.4 Requirements, problems, (dis)advantages

As I discussed in the previous sections, the core of a design explanation consists of two claims. One states that in certain conditions the traits in question are more useful to the organisms that have them than the alternate traits. The other claims that those conditions apply to the organisms concerned. Utilities are usually assessed in relation to functions$_2$ (causal roles). The utility claim, therefore, often takes the form of a claim about the utility of performing a certain function$_2$ (causal role) in a certain way. In the previous section I stated that claims about utilities may vary in strength. They may claim that the trait in question is the only one in the reference class that works (requirement claims) or they may claim that the trait in question is the best one in the reference class (optimality claims). Most design explanations do not merely claim *that* the trait in question is more useful than the other traits in the reference class, they also make plain *why* this is the case. This elaboration is the subject of the present section. I distinguish between requirement explanations and optimality explanations.

Requirement explanations

Requirement explanations explain why a certain trait is needed by identifying a problem into which an organism would run if it lacked the trait in question. The problem consists in a certain requirement not being met. For example, Krogh points out that the inner cells of larger organisms would not get enough oxygen if those organism relied on diffusion alone. Note that the problem is not a problem that is experienced by the real organism. It is a problem that would arise if the trait in question in a real organism was replaced by one of the alternative traits. In other words, the problem is identified by comparison with a *hypothetical* organism. Claims about such hypothetical organisms are established by experiments or calculations. These experiments and calculations aim to show (1) that and (2) why such a hypothetical organism would not be able to survive and reproduce / to perform a certain causal role, and (3) that and how the addition of the trait to be explained would solve this problem. The result of this analysis is expressed in a functional counterfactual of the form “if s-organisms had one of the alternative traits instead of the trait in question they would have problem *P*”.

An example of a viability explanation along these lines is the explanation of why vertebrates have (rather than lack) a circulatory system (suggested by Krogh):

(1) the distance between the inner organs and the periphery of vertebrates is more than 1 mm.

(2) for all organisms: if the distance between the inner organs and the periphery is more than 1 mm they need a system of convection in addition to diffusion.

(3a) in Vertebrates the circulatory system provides a system of convection in addition to diffusion.

(3b) if Vertebrates lacked a circulatory system they would not have a system of convection.

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(4) that's why Vertebrates have a circulatory system.

The first statements specifies certain conditions in which vertebrates live. The second states a requirement which applies in these conditions. The third and the fourth stated that this requirement is met if the trait in question is present but not if it is absent.

More generally, viability explanations have the following structure:

(1) s-organisms live in condition c_u.

(2) in condition c_u organisms can survive and reproduce only if requirement r is met.

(3a) if s-organisms have / perform t_1 requirement r is met.

(3b) if s-organisms have / perform t_2 requirement r is not met.

……

(3n) if s-organisms have / perform t_n requirement r is not met.

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(4) that's why$_2$ *s*-organisms have / perform t_1 rather than t_2, t_3, ..., or t_n.

Schwenk's (1994) explanation of why snakes have a forked tongue is an example of an explanation that appeals to what is required to perform a causal role:

(1a) Snakes and lizard use their tongue to sample chemicals

(1b) Snakes and lizards follow trails by comparing chemical stimuli simultaneously sampled at two points

(3) In order to compare chemical stimuli simultaneously sampled at two points an organism must be able to sample chemical stimuli simultaneously at two points

(4) In snakes and lizards this requirement is met if the tongue is forked but not if it is blunt

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(5) That's why the tongues of snakes and lizards are forked rather than blunt

The first two statements are function$_2$ attributions (attributions of causal roles). I have labelled them (1a) and (1b) to emphasize that they have the same character. The third one states a requirement. One might call this kind of statement an 'attribution of a need'. In this case the need / requirement is not conditional, so there is no need for a specification of the conditions in which snakes and lizards live. I have labelled the requirement claim (3) because this facilitates comparison with the general structure (to be presented shortly) which provides for a specification of the conditions in which the organisms in question live. The fourth statement says that this requirement is met if the organism has the trait in question but not if it has one of the alternative traits.

The general structure of a design explanation of the structure of an item by appeal to what is required to perform a certain function$_2$ (causal role) is:

(1) In *s*-organisms: item *i* performs causal role (function$_2$) *f*.

(2) s-organisms live in condition $c_{u.}$

(3) in condition c_u: causal role *f* is physical possible only if requirement *r* is met.

(4a) in *s*-organisms: if item *i* has character s_1 then requirement *r* is met.

(4b) in s-organisms: if item *i* has character s_2 then requirement *r* is not met.

……

(4c) in s-organisms: if item *i* has character s_n then requirement *r* is not met.

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(5) That's why$_2$ in *s*-organisms item *i* has structure s_1 rather than s_2, s_3, ..., or s_n.

Requirement explanations often point out a problem without mentioning the relevant requirement explicitly. In that case one gets something like:

(1) s-organisms live in condition $c_{u.}$

(2a) in condition c_u: if organisms had / performed t_2, $t_{3,}$ ..., or t_n instead of t_1 problem *p* would occur.

(2b) in s-organisms: if t_1 is present problem *p* does not occur.

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(3) that's why$_2$ *s*-organisms have / perform t_1 rather than t_2, t_3, ..., or $t_{n.}$

For example:

(1) In vertebrates the distance between the inner organs and the periphery is more than 1 mm.

(2a) If the distance between the inner organs and the periphery is more than 1 mm vertebrates would not be able to meet their demand for oxygen if they had to rely on diffusion alone.

(2b) the presence of a system of convection would solve this problem.

(3) in Vertebrates the circulatory system provides a system of convection in addition to diffusion.

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(4) that's why Vertebrates have (rather than lack) a circulatory system.

Actually, as indicated by the numbers, this example is more complex than the abstract scheme says. It starts with stating the conditions that apply to the organisms in question (vertebrates) (1). The second statement (2a) points to a problem these organisms would have if they lacked the trait in question (a circulatory system). The third statement (2b) points out a requirement in the form of a general solution to this problem (namely having a system of convection in addition to diffusion). The fourth statement (3) states how this general solution is implemented in vertebrates.

In sum: requirement explanations point out a problem the organisms in question would have in the conditions in which they live if the trait in question were replaced by one of the alternative traits. A problem means that a certain requirement is not met. The ultimate requirement is that the organism is viable and productive, but in many cases the explanation mentions a requirement which is derived from this ultimate one.

Optimality explanations

Optimality explanations proceed in a similar way. They point out that the organisms in question *would* have certain disadvantages in the conditions in which they live if the trait in question *were* replaced by an alternative. The ultimate disadvantage is that their fitness would be lower if the organism had an alternative instead of the trait in question. In many cases the explanation employs another criterion such as the efficiency by which a certain function$_2$ (causal role) is performed. This criterion is supposed to correlate with fitness.

An example of such an explanation is the explanation of Tinbergen and his students (1962) of why black-headed gulls remove the empty egg shell after the chick has hatched. This example was discussed in section 2.2.3 (example 3.1). This example can be represented as follows:

(1) The eggs of black-headed gulls are subject to predation by herring gulls and carrion crows.
(2) In the condition that eggs are predated by herring gulls and carrion crows it is useful to minimize the risk that the nest is discovered by herring gulls and carrion crows.
(3) The nest is less easily discovered by herring gulls and carrion crows if the empty shells are removed than if they are left.

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(4) That’s why$_2$ black-headed gulls remove the empty egg shell rather than leave it near the nest.

The first sentence states a condition in which the organisms in question live. The second states a utility criterion which applies in these conditions. The third sentence states that on this criterion the trait in question is more useful than the alternative traits.

Optimality explanations often point out disadvantages directly, without mentioning an explicit utility criterion. In that case the explanation has the following structure:

(1) s-organisms live in condition c_u.

(2a) in condition c_u if organisms had / performed t_2 instead of t_1 problem p_1 would occur.

(2b) in condition c_u if organisms had / performed t_3 instead of t_1 problem p_2 would occur.

….

(2n) in condition c_u if organisms had / performed t_n instead of t_1 problem p_o would occur.

(2o) in s-organisms: if t_1 is present problem $p_1, \ldots, p_o$ do not occur.

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(3) that's why$_2$ *s*-organisms have / perform t_1 rather than $t_2, t_3, \ldots,$ or t_n.

For example:

(1) The eggs of black-headed gulls are subject to predation by herring gulls and carrion crows.

(2a) in this situation the presence of an empty egg shells near the nest would endanger the brood.

(2b) as this "betrayal effect" decreases rapidly with an increasing distance between eggs and shells this problem is solved by carrying the egg shell away.

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(3) that's why$_2$ black-headed gulls remove the empty egg shell rather than leave it near the nest.

8.2.5 Appeal to physical laws

There is still one element missing in my account of design explanations (functional explanations$_2$), namely appeal to physical laws. Many design explanations, especially in functional morphology, derive requirements from the laws of physics and chemistry. A typical example is Krogh's derivation of why "larger" animals need a system of convection in addition to diffusion from Fick's law of diffusion. This explanation can be schematically represented as follows:

(1) According to Fick's law of diffusion the rate of diffusion depends on the distance of diffusion, the area available for diffusion, the concentration gradient of the diffusing gas and the diffusion coefficient of the medium in which diffusion takes place according to the following formulae: $J = -D A \, \mathrm{d}P/\mathrm{d}x$.

(2) The need for oxygen in vertebrates is such and such, the diffusion coefficient for animal tissue is $2 \cdot 10^{-5}$ mm^2/atm*s, etc.

(3a) If the distance between the inner organs and the periphery is more than 1 mm vertebrates would not be able to meet their demand for oxygen if they had to rely on diffusion alone.

(3b) the presence of a system of convection would solve this problem.

(4) in Vertebrates the circulatory system provides a system of convection in addition to diffusion.

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(5) that's why Vertebrates have a circulatory system.

This explanation starts with a physical law (1), next (2) it interprets the quantities in this law in terms of the organism (the oxygen supply at a certain point in the body of an organism is determined by the rate of diffusion, for an organism that has to rely on diffusion alone the relevant distance is that between the organs and the periphery and so on) and fills them out. From this it is calculated that an organism that lacks the trait in question would have a certain problem (3a), and that the presence of the trait in question solves this problem (3b/4).

8.3 Fundamental relations

8.3.1 Introduction

In the previous section I discussed the structure of design explanations (functional explanations$_2$). In this section I discuss the kind of relation with which such explanations are concerned. My two main claims are:

(1) design explanations are concerned with relations of functional interdependence between the parts, processes, behaviours of individual organisms and the environment in which they live (not with the causes of traits);

(2) relations of functional interdependence are constitutive of the structure of the living world.

As said before, my main question is the question what design explanations add to our knowledge. In order to answer this question it is worth paying some attention to the question what causal explanations add to our knowledge. Imagine a situation in which you know all events that happened in a certain space, in a certain period of time. Among other things you know that last week Roger woke up at seven except on Sunday, when he woke up at nine. What insight would be gained if someone causally explained the fact that on Sunday Roger woke up at nine rather than at seven by pointing out that his alarm clock broke down? The insight that there is a connection between the buzzing of the alarm clock and Roger's waking up, of course. You learn that the buzzing of the alarm clock is one of the factors that brings about Roger's waking up. More generally, it seems that causal explanations show us how a certain event, state or capacity hangs together with another part (event, state or capacity) of the world.

This is the position defended by Wesley Salmon in, among others, his *Scientific Explanation and the Causal Structure of the World* (1984). On Salmon's view explanations show us how a certain event fits into the causal structure of the world. As he puts it later:

> [a causal explanation] seeks to provide a systematic understanding of empirical phenomena by showing *how* they fit into a *causal* nexus (Salmon 1989: 120).

Salmon's causal theory of explanation is a special version of a more general view which is called "the ontic conception of explanation". According to the ontic conception explanations show us how a certain phenomenon fits into the structure of the world (causal or otherwise):

> According to the ontic conception [...] the explanation of events consists in fitting them into the patterns that exists in the objective world [...]. We all maintain that explanations reveal the mechanisms, causal or otherwise, that produce the facts we are trying to explain (Salmon 1989: 121).

Proponents of the causal version of the ontic view of explanation (such as Salmon) maintain that the structure of the objective world consists of causal relations only and that, hence, explanations must be causal; proponents of other versions of the ontic conception (such as Coffa and Railton) are more lenient towards non-causal explanations.

The view I will defend is kindred to the ontic conception. I argue that design explanations contribute to our knowledge because they show us how a certain trait of an organism relates to the other traits of that organism and the state of the environment in which it lives. However, the relation is not in terms of causes but in terms of what is useful for the organism to have.

On my view, explanations, in general, aim to show us how a certain phenomenon fits into the structure of the world. That is, they show us how that phenomenon hangs together with the rest of the world (as we know it). Of course, not any relation between phenomena is part of the structure of the world. For example, the relation '... is longer than ...' is not part of the structure of the world: if one shows that Peter is longer than Mary one does not show how Peter and Mary hang together. The question what kind of relations constitute the structure of the world is a scientific issue, that is it is answered in the course of scientific enquiry. The best indication that a certain kind of relation is part of the structure of the world is that it enables us to reach our practical and cognitive purposes. For example, we learn that causal relations are constitutive of the structure of the world both because they are the kind of relations which enable us to influence the course of events and because they enable us to build a unified science.

Proponents of a causal theory of explanation (e.g. Salmon 1984) maintain that the structure of the world is of a causal nature. I argue that, to our best knowledge, relations of functional interdependence too are part of the structure of, at least, the living world.[9] My main argument is that these relations determine which organisms are physical possible (i.e. able to survive and reproduce) and which not. For example, organisms in which the distance between the inner organs and the periphery is greater than 1 mm are not viable if oxygen transport is by diffusion alone. Such organisms must have an active transport mechanism: if they lack such a system they will die. In other words, the possession of a circulatory system makes it possible that an

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[9] Functional interdependencies are part of the structure of the world of artefacts, too. However, the investigation of artefacts is beyond my subject.

organisms becomes larger. We learn that such relations are constitutive of the structure of the world when we try to build an artefact. Whereas causal relations are the kind of relations that determine what things can be brought about, functional interdependencies are the kind of relations that determine what constructs are stable. Functional interdependencies are the kind of relations that enable us to build stable constructs.

In section 8.3.2 I describe the received view of the structure of the living world. This view distinguishes two kinds of causes: proximate causes which explain how organisms develop and maintain themselves and ultimate causes which explain why and how the different organisms evolved. The *locus classicus* for this view is Ernst Mayr's "Cause and Effect in Biology" (1961). In section 8.3.3 I propose to replace this dichotomy by a tripartition consisting of (i) causes at the individual level, (ii) causes at the population level and (iii) functional interdependencies. In section 8.3.4 I attempt an account of the relation of functional interdependence and in section 3.5 I discuss the relation between these three kinds of relations.

8.3.2 Mayr's distinction between proximate and ultimate causes.

Many evolutionary biologists tend to divide biology into two kinds: two fields or modes ("functional biology" and "evolutionary biology"), dealing with two different types of questions ("how questions" and "why questions") and two different types of causes ("proximate causes" and "ultimate causes"). For example, Futuyma (1986: 286), the "bible" of evolutionary biology, says:

> The study of biology may be divided into two modes. 'Functional biology' asks how an organism works—how does it develop and maintain itself? The other approach to biology, the historical approach, asks 'how and why has life come to be this way?'

The *locus classicus* for this division is Ernst Mayr's "Cause and Effect in Biology" (1961). In this influential paper Mayr contends that "the word *biology* is a label for two largely separate fields which differ greatly in method, *Fragestellung*, and basic concepts" (p. 1501). Functional biologists are said to ask 'how' questions and deal with proximate causes; they study physiological processes, favour the reductionist approach and reach their conclusions by means of experimentation. Evolutionary biologists are said to ask 'why' questions and deal with ultimate causes; they study biological diversity and use the comparative method.

This view of biology has its historical roots in the successful attempt of Dobzhansky, Mayr, Simpson and Stebbins to frame the study of evolution as a professional science. Among other problems they had to deal with the prevailing view that biology should aim to reduce biological phenomena to physical processes, if it was to be taken seriously as a science. The proximate / ultimate distinction was Mayr's answer to this problem. This distinction should at once confirm the autonomous character of biology and the legitimacy of evolutionary biology as a science.

Science according to Mayr aims to discover the causes of what happens. However, in the living world almost any phenomenon has two sets of causes: a proximate set and an ultimate set. The proximate set is the object of traditional biology (physiology or functional biology, as Mayr called it), the ultimate set was to be the object of the new study of evolution. A complete explanation would identify both sets, and both studies are therefore equally legitimate.

As Mayr repeatedly emphasizes neither the terms 'proximate cause' and 'ultimate cause' nor the idea that biology has two sides were new. Mayr, however, was the first who attempted a more systematic treatment of these concepts and who made them into the foundation of biology.

Mayr introduces his proximate / ultimate distinction by means of an example, namely the question why a certain warbler individual started to migrate southward on August 25th (Mayr 1961: 1502/3). Mayr lists four causes for this migration:

(1) "an intrinsic physiological cause": in response to a decrease in day length the warbler became physiologically ready to migrate in response to certain weather conditions;
(2) "an extrinsic physiological cause": the weather conditions on August 25 were such that the warbler, already physiologically ready for migration, started off that day;
(3) "a genetic cause": in the course of evolution the warbler has acquired a genetic constitution that induces the appropriate physiological response to environmental stimuli;
(4) "an ecological cause": "the warbler, being an insect eater, must migrate, because it would starve to death if it should try to winter in New Hampshire".

According to Mayr "we can readily see" that these causes fall into two types. The physiological causes might be called the proximate causes; the other two the ultimate causes.

Note that Mayr's use of the term 'cause' is ambiguous. The term is often more or less synonymous with 'explanation' (or with 'causal explanation') but in some places it is better interpreted as meaning 'the conditions that brought about a certain effect' (that is as 'cause' in a more usual sense).

In order to clarify the distinction between proximate and ultimate causes Mayr invokes the notion of a 'genetic program'. According to Mayr proximate causes are the explanations that deal with the decoding of the genetic program. Ultimate causes, on the other hand, are "the causes that have a history and that have been incorporated into the system through many thousand generations of natural selection". I assume that he means that ultimate explanations deal with the history of the genetic program.

The notion of a 'genetic program' is controversial. Mayr does not explain this notion and answers the objection that this notion is unclear by saying that it is well established in biology. This answer is unsatisfactory but that need not distract us. Mayr's distinction can be made without using the notion of a genetic program: proximate explanations are concerned with the mechanisms that bring about a certain reaction in a certain individual; ultimate explanations seek to explain the differences between the mechanisms of individuals of different taxa. In later work

Mayr uses the terms “ultimate”, “evolutionary” and “historical” as synonyms (e.g. Mayr 1982: vii, 67) as do his followers. Brandon (1981: 93) for instance, states that ultimate explanations answer the question “how and why has this mechanism evolved”. In a recent book Mayr says that “evolutionary (historical or ultimate) causes [...] attempt to explain why an organism is the way it is, as a product of evolution” (Mayr 1997: 117).

Table 3.1: design explanations do not fit into Mayr’s classification of explanations

proximate explanation (Mayr)	ultimate explanation (Mayr)	design explanation (as I have shown)
concerned with proximate causes	concerned with ultimate causes	concerned with utilities
functional biology	evolutionary biology	functional biology
physiological processes	biological diversity	(differences in) form, activity, behaviour
answers how-question	answers why-question	answers why-question
reductionist	historical	holistic
employs physical sciences	employs population genetics	employs physical sciences
concerned with the decoding of a genetic program	concerned with the history of a genetic program	concerned with the interrelation between the parts and behaviours of organisms and their environment
how things work	how and why things evolved why things are the way they are	how things hang together why things are the way they are
experimentation	comparison	comparison, experimentation and calculation

Mayr's insight that there are two equally legitimate and complementary ways to fit biological phenomena into the causal structure of the world has been a major breakthrough in the philosophy of biology. In my proposal in the next section I take this insight into account as the distinction between individual level causal explanations and population level causal explanations. However, Mayr’s account fails to do justice to design explanations (see table 3.1) and confuses them with evolutionary explanation.

As I have argued design explanations address the questions why an organism is as it is, but they answer this question not in terms of their evolutionary history but in terms of what is useful to survive and reproduce. Design explanations are also used to explain the differences between the mechanisms in individuals of different taxa, but they point to the different needs which the different mechanisms should satisfy, not to the different histories of those mechanisms. Design explanations are holistic in character (they explain individual level traits in terms of other individual level traits) but they are established by means of experimentation and calculation, and they show an orientation towards the physical sciences.

Mayr's own example of an ecological cause. According to Mayr ultimate causes are “the causes that have a history and that have been incorporated into the system through many thousand generations of natural selection”. However, Mayr's example of an ecological cause is a clear case of a functional counterfactual: “the warbler, being an insect eater, *must* migrate, because it *would* starve to death *if* it should try to winter in New Hampshire”. It relates the warbler's migration (the trait to be explained) to its eating habits (“being an insect eater” is the explaining trait) in terms of needs (“the warbler would starve to death”). The truth of this counterfactual is established by experimentation and calculation and has nothing to do with how the warbler and its traits evolved historically. The view of cold winters as the ultimate and historical cause of migration easily gives rise to the misunderstanding that warblers evolved the habit of migration as the result of thousands of years of insect eating in a seasonal climate. Of course, this scenario is wrong. The warbler's ancestors must have been migrating either before they started to live exclusively on insects or else before they moved to a seasonal climate. The fact that an insect eater would starve to death if it did not migrate, however, only explains why insect eaters must migrate (if they are not to starve) not why migrating insect eaters evolved. It seems therefore appropriate to distinguish design explanations from evolutionary explanations rather than to lump them together under the banner of “ultimate causation”.

8.3.3 My proposal

In order to accommodate design explanations I propose to classify the relations to which explanations in biology appeal (the relations that constitute the structure of the living world) along two dimensions: (1) individual level / population level relations, and (2) causes / interdependencies. This results in the following tripartition: (i) causes at the individual level, (ii) causes at the population level, and (iii) functional interdependencies at the individual level. The question whether there exist functional interdependencies at other levels than the individual (e.g. at the population level or at the level of the ecosystem) and what their role is in biology is irrelevant to my subject and for that reason ignored.

Note that, in contrast to Mayr, I clearly distinguish between explanations and the relations with which those explanations are concerned.

Individual / population

The importance of the distinction between relations at the individual level and relations at the population level has been stressed recently by Ernst Mayr, Richard Lewontin and Elliott Sober. These authors emphasize that the insight that evolution is essentially a population phenomenon is one of the major breakthroughs Darwin brought about. Lewontin (1981, 1983) points out that Darwin conceived of evolution in a manner that is radically different from conceptions of historical change before Darwin. Lewontin distinguishes two ways of conceiving of historical change. Before Darwin theories of historical change were *transformational* in nature. That is, they accounted for evolution in terms of individual transformations. For instance, in Lamarck's theory of evolution species change because the organisms in them are gradually modified. Darwin's theory on the other hand is *variational* in character. In this view it is the population rather than the individual that evolves. The population is made up of individuals that differ from each other in some properties and the population evolves by a change in the proportions of the different variants (whereas the individuals may remain the same). (See also Sober 1984: 147-155).

Darwin's emphasis on populations and on individual differences was first brought to our attention by Mayr in his essay "Typological versus Population Thinking" (1959). Mayr summarizes Darwin's innovation as follows:

> For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real (Mayr 1976: 28).

Sober (1984: 155-169) elaborates on Mayr's ideas. Following Mayr, he distinguishes two views on variation. In the "typological" or "essentialist" view variation between organisms is conceived of as the result of forces acting on the individual. These forces drive the individual away from a natural state, thought to be typical of a species (the natural state is called the "type" of that organism or of that species). In the Darwinian view, on the other hand, variation is a natural state of populations rather than a deviation of individuals. The discipline that studies the principles of variation is called "population genetics". Population genetics employs a natural state model. This model is the Hardy-Weinberg model, which describes how a population behaves in the absence of "disturbing forces" like selection and drift. This Darwinian view differs from the typological view in several aspects. First, variation itself is viewed as a natural state rather than as a deviation from the natural state. Second, natural states are states of populations rather than of individuals. Third, evolution essentially involves processes (such as selection, drift and hybridization) that work at the population level in addition to processes that work at the individual level (such as mutation and recombination).[10]

Causes / interdependencies

Design explanations differ from causal explanations in that they are not concerned with how a certain event, state, trait or capacity is brought about but with functional interdependencies. Functional interdependencies are synchronic relations which determine which combinations of characters are stable (can survive and reproduce) and which not. It was, once more, Darwin who paved the way to the insight that design explanations do not explain how a trait came into being. In the pre-Darwinian traditions of Cuvier and Von Baer it was supposed that the needs a trait satisfies causally explain the emergence and maintenance of that trait at the individual level. The biologists working in these traditions were impressed by the interdependence of the different parts and processes of an organism. The harmony of the different parts of an organism was understood as the result of the interaction of the needs of that organism at the individual level. According to George Cuvier (the founding father of functional morphology) the two basic principles of zoology are the principle of the conditions of existence and the principle of the correlation of parts. The principle of the conditions of existence states that the different parts and processes depend on each other and support each other.

> Since nothing can exist without the reunion of those conditions which render its existence possible, the component parts of each being must be co-ordinated in such a way as to render possible the whole being, not only in itself, but also with regard to its surrounding relations (Cuvier 1817, vol. 1: 6).

As a result there are certain regularities in the design of organisms: certain organs are always found together and from the form of a certain organ one can infer the presence and the form of certain other organs (this is the principle of the correlation of parts). For example, if the alimentary canal of a certain animal is suitable for digesting flesh (and nothing else) the other organs of the animal must also be adapted to this particular process. The organism must be capable to obtain this kind of food and to process it. The animal will be a fast runner. It will have fangs and carnassial teeth, strong claws and muscles, keen sight, fine smell, and a stream-lined body. Such correlations are to be determined by means of comparative anatomy. According to Cuvier all factual correlations are the result of functional interdependencies. Some correlations, such as that of a carnivorous alimentary canal and strong claws, are explicable on “rational grounds”, which means that by means of plausible reasoning one is able to show that an animal having a

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[10] In population genetics evolution is often defined as a change in the gene pool of a population over time. The gene pool is the set of all alleles ("genes") in a population. Some authors (e.g. Endler 1986) have objected to the population genetic definition of evolution, but they do not the deny that evolution is a population phenomenon.

certain trait (e.g. a carnivorous alimentary canal) needs certain other traits (e.g. claws). But even correlations that are not explicable on rational grounds, such as the correlation between being ruminate and having cloven hoofs, must be accepted as functional interdependencies on “empirical grounds”.

The question ‘how did the different parts and processes of an organism became geared to each other?’ became one of the central theoretical issues in eighteenth and nineteenth century biology. As is well-known, in British Natural Theology this question was answered by appealing to the hand of a benevolent creator. In main stream biology this doctrine never made headway. Cuvier saw the harmony between the different parts and processes of an organism as the result of the causal interaction of the interdependent parts at the individual level. This interaction was assumed to be a kind of material exchange, called “tourbillon vitale” (“Stoffwechsel” in German). Interdependent parts were thought to maintain each other by means of this “tourbillon vitale”. The same process operates in development and regeneration. Cuvier and his followers tend to confuse this assumed causal interaction between functionally interdependent parts with the relation of functional interdependency itself. In their view the fact that several organs are functionally interdependent maintains the gearing between those organs. The needs of an organism (such as the need for strong claws in an organism capable of digesting only flesh) act as efficient causes which organize the process of material exchange in such a manner that the organism’s needs are satisfied. Hence, design explanations (which appeal to the need for a certain structure) are seen as causal explanations, they explain how the harmony between the parts and the processes of an individual organism is maintained.

The process of material exchange was thought to explain (in principle) how the harmony of an organism is maintained. The origin of this harmony is another issue. According to these biologists causal interaction in the organic world differs from causal interaction in the non-organic world. Causal interactions in the non-organic world were supposed to be linear, (A->B->C->D), causal interactions in the organic world are “clearly” cyclic (A->B->C->A). In the view of late eighteenth, begin nineteenth century science it is impossible to explain how such a cyclic arrangement of causes came into being.[11] What we can try, however, is to explain how this arrangement is maintained (in the individual) and modified (in the course of the ontogeny) given the fact that there is such an arrangement.

This is were Darwin comes in, or rather his theory. Darwin, himself had a poor grasp of the theoretical issues in contemporary morphology, among others because he had no formal training in biology. He also had difficulties in understanding German, which was the language of biology in that time. Darwin addresses the issues raised in the tradition of natural theology and focuses on biogeographical, taxonomic and ecological questions, rather than on theoretical

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[11] This view is most clearly expressed in Kant’s *Kritik der Urteilskraft* (1790).

morphology. When he speaks of ‘adaptation’ he is either concerned with the relation between an organism and its external environment or with the efficiency with which a specialized organ performs its causal role. Darwin seems unaware of the issue of functional interdependencies. At least, he does not explicitly discuss this issue. However, the upshot of Darwin’s work is that the answer to the question ‘how did the parts and organs of an organism became geared to each other and to the environment in which it lives?’ must be sought in the evolutionary history of the lineage rather than in immediate causal interaction between the parts that are in harmony.

In modern biology the metabolic interaction (if any) between two functionally interdependent organs does not explain the gearing of those organs. Harmony between parts and processes is “pre-stabilized” in the genes. For instance, the lungs of birds have a very complicated structure which is needed to enable flight. In the view of Cuvier, Von Baer and their followers, this harmony is established and maintained by a metabolic process operating between the lungs and the wings of the individual that has both items. In the view of modern biology there is no such exchange. In the course of the ontogeny the lungs and the wings acquire their structure independently. The fact that these structures are in harmony is explained by the fact that in the course of evolution the structures of wings and lungs became tuned to each other (due to selection).

For our purposes, the point is that in Darwin’s trail it became clear that it is important to distinguish explicitly not only between individual level and population level relations but also between individual level causal relations and individual level functional interdependencies (needs, demands and utilities).

Classification of explanations

If the two dimensions (individual / population, causal / functional) are combined one gets four kinds of fundamental relations: (1) causal relations at the level of the individual, (2) causal relations at the level of the populations, (3) functional interdependencies at the individual level, (4) functional interdependencies at the population level. Relations of the fourth kind are not relevant to functional biology (which is primarily concerned to explain the form, activity and behaviour of individual organisms) and for that reason, I will ignore this kind of relations. The resulting tripartition of fundamental relations gives one a better grip on the nature of the relations which are the subject of the different kinds of explanation I discussed in chapter 2 (better than Mayr’s bipartition).

Physiological explanations (the kind of explanations which biologists call ‘causal explanations’) are concerned with individual level causal relations. These come in two kinds: explanations that specify causes for a certain type of change, and explanations that specify properties (among which are capacity explanations, that is functional explanations in Cummins’s sense).

Design explanations (the kind of explanations which biologists call ‘functional explanation’) are concerned with functional interdependencies at the individual level. They explain why it is useful to a certain organism that a certain item or behaviour has a certain character or why it is useful to that organism that a certain causal role is performed by relating that utility to the state of that organism and the environment in which it lives. They explain why a trait is useful to certain kinds of individuals, but they do not explain how that trait was brought about in those individuals. Neither do they explain how that trait was brought about in evolution.

Developmental explanations are concerned with causes at the individual level (just as physiological explanations). They show us how the ovum changes into the adult individual and what the mechanisms are that bring about this change.

Evolutionary explanations are concerned with causes at the population level. They explain how the current state of the population was brought about by a series of changes in an ancestral population. They might also explain the mechanism of change.

Table 3.2 shows the differences between the three kinds of explanations which philosopher’s call ‘functional explanations’.

Table 3.2: Different types of so-called “functional explanations” and their characteristics.

	level	**nature**	**strategy**
Selection explanation	population (lineage)	causal relations	historical
Design explanation	individual	functional interdependencies	holistic
Capacity explanation	individual	causal relations	reductionist

8.3.4 Functional interdependencies

The concept of need

Design explanations are virtually ignored in contemporary philosophy of science, and to the extent that they receive attention they have been confused with capacity explanations or with evolutionary explanations. The nature of the relation of functional interdependence has received no attention at all in contemporary philosophy of science. This in contrast to the nature of causation, which has been the subject of heated debate. In this section I offer a first attempt to analyze the nature of functional interdependence. I develop this analysis by means of an example.

My example concerns the shark’s spiracle. The spiracle is an oval opening which appears to lie just before the gill slits. Among biologists it is well known that the spiracle actually *is* a (modified) gill slit.[12] In contrast with the other gill slits, the spiracular slit is used for the *inflow* of water. The answer to the question why$_2$ sharks need a spiracle appeals both to the shark's need for oxygen and to the feeding habits of sharks. To satisfy the shark's need for oxygen a continuous flow of fresh water over the gills is required. Normally this flow is supplied via the mouth, but when the shark has caught a large prey this channel is blocked. The spiracle affords a channel for the inflow of water when the mouth is blocked. As I said, this design explanation explains the presence of a spiracle in terms of the need for oxygen and the feeding habits. It tells us that the spiracle is needed because the size of the prey makes it impossible to supply enough fresh water via the mouth. The traits to which a design explanation appeals are often said "to demand for" the trait in question. For example, the eating habits and the need for oxygen together demand for a spiracle.

However, a spiracle is not the only possible way to meet the demand for a continuous flow of fresh water over the gills. Lampreys manifest a different solution for the same problem. Lampreys attach themselves to their prey as a result of which they are unable to take in water via the mouth. Their solution is to take in water via the nose. Hence, the spiracle and the nose are functional equivalents.

In analyzing the notions 'needed' and 'demands for' I will apply some ideas put forward by John Mackie (1974). Mackie is concerned with the analysis of the notion of cause. Mackie views a causal relation as a necessary succession of events. His central problem is the distinction between necessary (i.e. causal) and accidental successions. Mackie envisages a chestnut which is treated with a hammer. In the example of a causal succession the chestnut lies on a flat stone and the chestnut is observably flatter after it is hit by the hammer than it was before. In the example of an accidental succession the chestnut lies on a red-hot iron plate and explodes at the moment it is hit by the hammer. Consider the question what makes the first sequence necessary and the second one accidental. Mackie says that "every intelligent and unbiased person" will answer this question by referring to the fact that in the first case the chestnut would not have flattened if it were not hit by the hammer, whereas in the second case the chestnut would have exploded anyhow. More generally his conclusion is that we do not speak of a necessary succession if we have no reasons for a counterfactual statement. In the case of causal relations the counterfactual states that in the given circumstances the effect would not have occurred if the cause were absent. In other words, according to Mackie in the circumstances a cause is necessary for its effect.

Mackie emphasizes that his analyses of a cause as necessary in the circumstances does not imply that the cause is indispensable in the circumstances (see also Mackie 1965). The events which are commonly labelled 'causes' are often neither indispensable nor sufficient for their

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[12] More precisely, it is the branchial opening lying between the mandibular and the hyoid gill arch.

effects. To take this insight into account he defines the notion ‘at least an INUS-condition’. An INUS-condition is an *i*nsufficient but *n*on-redundant part of a condition which is itself *unnecessary* but *s*ufficient for a certain effect”. The central notion of his analysis, however, is ‘at least an INUS-condition’, which is a non-redundant part of a sufficient condition (this notion differs from that of an INUS-condition in that it includes the cases in which the non-redundant part is sufficient, and in which the condition of which the non-redundant part is a part is indispensable). More formally this may be put as follows:

> An event of type A is *at least an INUS-condition* for an event of type P if and only if there are certain (usually unknown) conditions X, such that:

(1) AX[13] is sufficient for P, and
(2) X alone is not sufficient for P

The statement ‘A is a cause of P’ implies according to Mackie:

(1) A is at least an INUS-condition of P,
(2) both A and X were realized in the circumstances in which P occurred,
(3) all possible alternative sufficient conditions for P ($Y1$, $Y2$ and so on) were not realized in the circumstances in which P occurred.

A is non-redundant because X alone is not sufficient for P but not necessary indispensable because $Y1=KX$ might be another sufficient condition for P.

In the Hempel and Nagel approach, the question whether a trait is necessary or not is equivalent to the question whether the trait is indispensable or not. I think it is reasonable to say that needed traits are necessary although they are not indispensable. Needed traits are necessary in the sense that if the organism *as it is* would lack the trait it would not be able to survive and reproduce. More formally this may be put as follows:

> A trait A is *needed* in an organism *i* if and only if in *i* or in *i*’s environment a certain condition X is realized, such that:

(1) the realization of both A and X is sufficient for *i* to survive and reproduce, and
(2) X alone is not sufficient for *i* to survive and reproduce, and
(3) for all $Y \quad A$:[14] the realization of Y and X is not sufficient for *i* to survive and reproduce[15], and
(4) possible alternatives for A ($K1$, $K2$, etc.) are not realized in *i*.

---

[13] AX means: both an event of type A and condition X are realized. This condition is satisfied if an event of type A occurred.

[14] ‘$Y \quad A$’ means that A is a combination (“conjunction”) of conditions and Y is one of the parts (“conjuncts”).

[15] This condition is added in order to avoid that the combination of a needed condition (e.g. the presence of a spiracle in sharks) and an unneeded one (e.g. the white colour of its bones) counts as needed.

A is necessary because X alone is not sufficient for *i* to function adequately (a shark would die if it lacked a spiracle), but possibly dispensable because KX might be another sufficient condition (for example, K might be the intake of water via the nose).

This definition explains why counterfactuals have such an important role in design explanations. For example, compare a needed trait such as the spiracle of the shark, with a non-needed one such as the colour of its bones. How do we know that the spiracle is needed and the colour of its bones not? Consider an experimental set up in which the shark is fed large preys only. In this situation, if one would block the spiracle the shark would die, but if one would paint its bones purple this would not have any consequence for its survival. Hence, the need for a spiracle is revealed by an argument and/or an experiment which shows that the shark could not survive if it lacked the spiracle.

The relation 'demands for'

The relation 'B demands for A' is more difficult to characterize. The basic idea is that B demands for A if B is at least an INUS condition for the utility of A. Compare the relation between the feeding habits of the shark and the presence of a spiracle, with an accidental "relation", such as that between the cartilaginous character of the skeleton and the presence of a spiracle. The eating habits of the shark demand for a spiracle, but the composition of the skeleton is irrelevant to the need for a spiracle. Again the difference is expressed in terms of a functional counterfactual: if the shark did not eat large preys, a spiracle would not be needed, but the composition of the skeleton is irrelevant to the need for a spiracle.

Note, that in contrast with causal relations, such as 'brings about', the relation 'demands for' is not transitive. For example, the lack of small preys demands for a shark's habit to catch large preys and the habit to catch large preys demands for a spiracle. However, the lack of small preys does not (directly) demand for a spiracle: if there were enough small prey available and the shark would catch large prey, a spiracle would still be needed. A related difference between causal relations and functional interdependencies is this. Causes form a chain and the same event never occurs twice in a chain of causes (there is no backward causation), but functional interdependencies form a network and although most connections will have a direction (the habit to catch large preys demands for a spiracle but not the other way round) there is no direction at the global level. In order words: the transitive closure of the causal relation is a partial ordering but the transitive closure of the relation 'demands for' not.

As a first impulse one might want to spell out the idea that a certain trait demands for another trait in the following way:

First attempt. A certain condition B (realized in an organism i or in the environment in which i lives) *demands for* trait A of an organism i[16] if and only if in i or in i's environment a condition X is realized, such that:

(1) the realization of A, B, and X together is sufficient for i to survive and reproduce,
(2) B and X *together* are not sufficient for i to survive and reproduce,
(3) for all $Y \quad A$: the realization of Y, B, and X is not sufficient for i to survive and reproduce, and
(4) the realization of X alone is sufficient for i to survive and reproduce.

According to this definition the habit to eat large preys demands for a spiracle, but the cartilaginous character of the skeleton does not demand for a spiracle.[17] Which is desired.

However, this definition does not work for several reasons. One is that B itself might be needed in which case X alone might not be sufficient for i to survive and reproduce. In other words, if someone says that in i B demands for A this does not imply that i could live without A if B were not present. This problem is solved by the following definition:

Second attempt. A certain condition B (realized in an organism i or in the environment in which i lives) *demands for* a trait A of an organism i if and only if in i or in i's environment a condition X is realized, such that:

(1) the realization of A, B, and X together is sufficient for i to survive and reproduce,
(2) B and X *together* are not sufficient for i to survive and reproduce,
(3) for all $Y \quad A$: the realization of Y, B, and X is not sufficient for i to survive and reproduce, and
(4) for all Z (A / Z, B / Z): if an organism in which A, X and Z are realized is able to survive and reproduce then an organism in which X and Z alone are realized is able to survive and reproduce.

This definition says that "B demands for A" implies that A would be redundant if B were absent.

However, if there is a Z (A / Z, B / Z) such that AXZ is able to survive and reproduce and a part of Z demands for A then condition (4) is not satisfied. This is unwanted. For example, in the case of the shark the habit of eating large prey demands for a spiracle. Yet, there is a Z such that AXZ is able to survive and reproduce and XZ not: a bottom-dwelling shark without a spiracle would have problems maintaining the flow of water over the gills if it lays down on the

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[16] This is meant to imply that A is present in i.

[17] Suppose A is the presence of a spiracle and B the cartilinagous character of the skeleton. If condition (2) applies BX is not able to survive if the spiracle is absent. Since, the shark would be able to survive if it did not eat large prey, this means that X must include a condition that makes a spiracle necessary, such as the habit of eating large prey. But in that case (4) does not apply.

sand (the mouth lays on the sand then). This means that a bottom-dwelling shark with a spiracle is able to survive and reproduce, but a bottom-dwelling shark without a spiracle not. This example is not far-fetched. Skates and rays spend a large part of their life on the bottom of the sea, with their mouth more or less buried in sand or mud. These creatures have a very large spiracle which meets the need to maintain the inflow of clear water when they are buried. It appears that condition (4) is too strong. Apparently, 'B demands for A' means that B is part of a disjunction of conditions each of which might create the need for A. This brings me to the following attempt:

> *Third attempt*. A certain condition B (realized in an organism i or in the environment in which i lives) *demands for* a trait A of an organism i if and only if there is a set of conditions U ($B \quad U$)[18] and in i or in i's environment a condition X is realized such that
>
> (1) the realization of A, any U_i ($U_i \quad U$), and X together is sufficient to survive and reproduce,
>
> (2) the realization of any U_i ($U_i \quad U$) and X together is not sufficient to survive and reproduce,
>
> (3) for all Y ($Y \quad A$): the realization of Y, B, and X is not sufficient for i to survive and reproduce, and
>
> (4) for all Z (A / Z, no U_i / Z): if an organism in which A, X and Z are realized is able to survive and reproduce then an organism in which X and Z alone are realized is able to survive and reproduce.

This definition too has a problem. It might be the case that a certain trait is needed for more than one reason and that those reasons are independent of each other. Recall, the example of inquilinism in pearlfishes (example 4.1 of section 2.2.4). This behaviour is needed for two reasons: it is needed to avoid predators and it is needed to avoid light. This means that there are two conditions which independently demand for the inquilinistic behaviour, namely the presence of a certain kind of predators (U_1) and the absence of pigment (U_2). If one or both of those conditions itself is needed (1) does not apply. This brings me to my final attempt:

> *Fourth attempt*. A certain condition B (realized in an organism i or in the environment in which i lives) *demands for* a trait A of an organism i if and only if there is a set of conditions U ($B \quad U$) and in i or in i's environment a condition X is realized such that
>
> (1a) the realization of A, all U_i 's realized in i, and X together is sufficient to survive and reproduce,

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[18] '$B \quad U$' means that U is a disjunction of conditions and B is one of the disjuncts (B is a U). B might be the only (element of) U.

(1b) the realization of A, any U_i (U_i U and U_i not realized in A), and X together is sufficient to survive and reproduce,

(2) the realization of any U_i (U_i U) and X together is not sufficient to survive and reproduce,

(3) for all Y (Y A): the realization of Y, B, and X is not sufficient for i to survive and reproduce, and

(4) for all Z (A / Z, no U_i / Z): if an organism in which A, X and Z are realized is able to survive and reproduce then an organism in which X and Z alone are realized is able to survive and reproduce.

There is however one more problem. None of these definitions excludes that a combination of a relevant factor (say the habit too eat large preys) and an irrelevant factor (say the presence of a tail) demands for A (in our example the spiracle). This problem can, I think, be solved by requiring that if B demands for A then any V B demands for A. I am sure that there are further problems once we make the case even more complex. However, it is not the purpose of this chapter (and book) to work out this problem in further detail. The previous general analysis should suffice for the moment.

8.4 Design explanation and functional interdependencies

8.4.1 What is learned from a design explanation

Functional biologists are concerned with three kinds of fundamental relations: causal relations at the individual level, causal relations at the population level and functional interdependencies at the individual level. Design explanations are concerned with the latter kind of relations. Design explanations show their audience how the different parts of an organism, the form and activity of those parts, the behaviour of the organism are functionally dependent on each other and on the environment in which the organisms lives. I will discuss a number of examples to support this claim.

Consider for example the explanations concerned with circulation and respiration (section 4.2.3 and 6.2.2). These explanations show how the presence of a system of blood circulation with respiratory pigments relates to the physical characteristics of the diffusion process, to the size of the organism in question, to its need for oxygen (and therefore to its activity), to the physical characteristics of the blood, to the capacities of the pump and so on. They show how the form of a flatworm relates to the absence of a circulatory system. They relate the presence of respiratory organs and the form which they take to the size of the organisms in question, their need for oxygen, the physical characteristics of the environment in which they live, and so on.

Similarly, Habibi, Thouless and Lindsay (1993) (example 3.3 of chapter 2) relate behavioural differences between sand gazelles and mountain gazelles to each other, to the laws of probability, to physiological and physical characteristics of new-born gazelles and lactating offspring and so on (see fig. 81.)

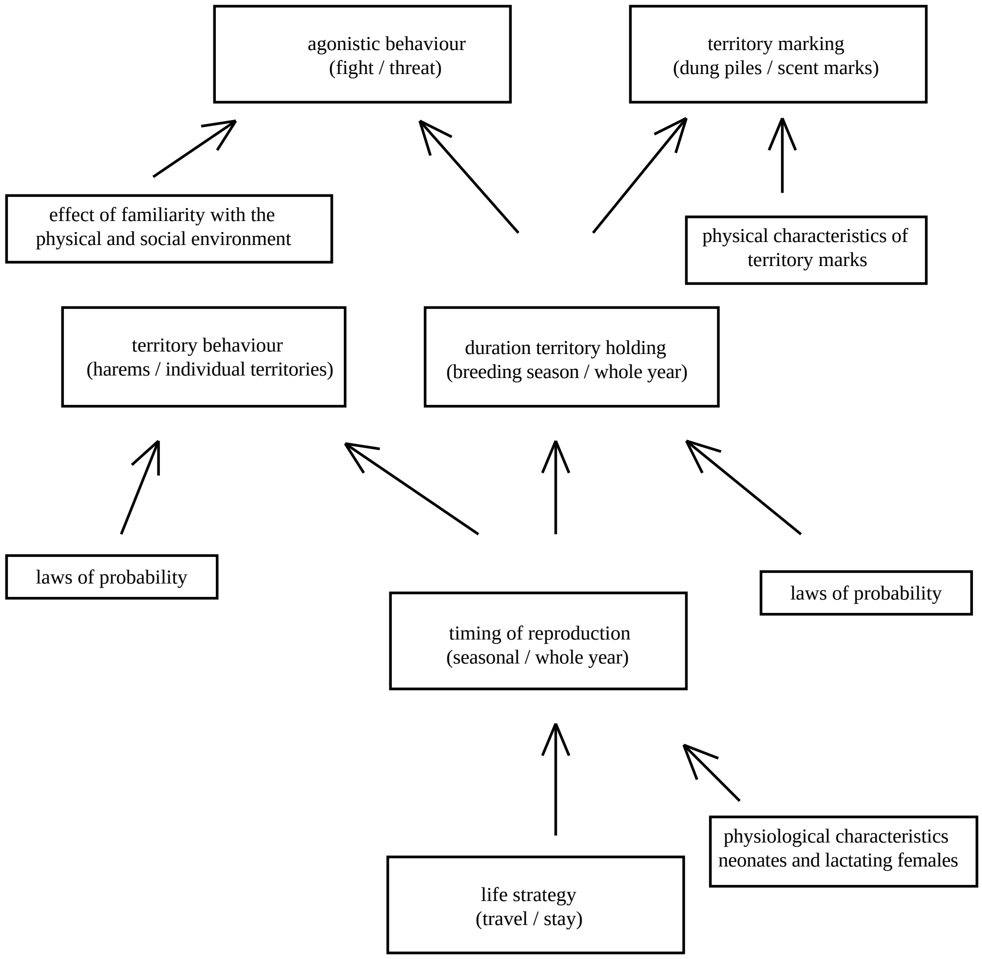

Fig 8.1: Differences between sand gazelles and mountain gazelles

In section 8.2 I discussed the structure of design explanations. Many design explanations are much more complex than the examples which I discussed in that section: typically they combine statements of several types. I now discuss three typical examples of complex design explanations. These examples connect the discussion of the structure of design explanations in section 8.2 to the main point of this section, namely that design explanations show us how things hang together in terms of what is useful to survive and reproduce. Furthermore, they illustrate three strategies to develop design explanations: (1) explain how a certain utility criterion is optimized or how a certain requirement is met, (2) pose a problem that would occur if the trait in question were replaced by an alternative trait and explain why this problem is a problem, (3) identify a complex task in which the item or behaviour the structure of which is to be explained takes part, make up a simple implementation and explain why this implementation does not work in the conditions in which the organisms in question live, pose a solution for this problem and repeat the process until one has developed a implementation similar to the structure to be explained.

Why mammals gallop

A straight forward way to explain why an organism is built the way it is built or why it behaves the way it behaves is this: pose an optimality criterion or a requirement that applies in the conditions in which the organisms in question live and show that an organism with the traits in question scores better on this criterion than an organism with the alternative traits or that an organism with the traits in question meets this requirement whereas an organism with the alternative traits would not meet the requirements. An example of such an explanation is McNeill Alexander's (1988) explanation of why mammals gallop. Most larger mammals (such as dogs, horses and antelopes) change gaits as they increase speed. At low speed the gait of these mammals is symmetrically: the left and the right leg of a pair swing in opposite directions (such as in walking and trotting). At high speeds they change to galloping, an asymmetrical trait in which both the forelegs swing in the opposite direction as the hindlegs. McNeill Alexander and his colleagues expected that large mammals gallop because galloping minimizes the energy costs of fast locomotion. The first attempts to work out this idea by means of mathematical modelling seemed to refute it: the models appeared to show that, even at high speeds, there always is a symmetrical gait that is at least as economically as galloping. However, metabolic measurements showed that in the range of speeds at which horses normally gallop, galloping is *de facto* more economically than any other gait. It remained a riddle why this is the case, until the researchers realized that the aponeurosis of the backbone could serve as a strain energy store. As an animal increases its speed, the fluctuations of the internal kinetic energy of the legs become larger. At a certain speed it becomes useful for the organism to balance these fluctuations by storing strain energy. McNeill Alexander and his colleagues had previously rejected the possibility that elastic items could help to save energy by balancing energy fluctuations. They now show that their previous objection holds only if the organism's gait is symmetrical. If the gait is asymmetrical (such as in galloping) the aponeurosis can serve to store energy. Thus, the explanation of why large mammals change from symmetrical gaits to galloping at high speeds is probably that this change enables the animal to store strain energy in the aponeurosis, which saves energy at high speeds and only at high speeds.

The train of thought of this explanation can be represented schematically as follows:

(1) It is useful for an organism to perform a certain activity with as less energy costs as possible.

(2) At high speeds it becomes possible for large mammals to save energy by storing strain energy, whereas at low speeds storing strain energy does not pay much.

(3) The aponeurosis of the vertebral column of large mammals serves as a strain energy store.

(4) The aponeurosis can perform this causal role (function$_2$) if the gait is asymmetrical but not if it is symmetrical.

(5) Galloping is an asymmetrical gait whereas trotting and walking are symmetrical

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(6) That's why large mammals gallop at high speeds rather than trot or walk

This explanation starts by stating a general criterion for what counts as useful, namely to perform a certain activity with as less energy costs as possible (1). Next, it points out a way to implement this criterion (by storing strain energy). It is also emphasized that this implementation would be useful only in the conditions in question (at high speeds) (2). Then, it points out an item that implements the causal role mentioned in (2), namely the aponeurosis of the vertebral column (3). Sentence (4) states a requirement that applies if the item is to perform that causal role. Statement (5) points out that in the condition stated in (2) the trait in question meets the requirement stated in (4).

This explanation relates the habit to gallop to the way in which larger mammals are built, to the conditions in which this habit takes place, and to the laws of mechanics.

Photoreceptor twist

In the example above, McNeill Alexander and his colleagues had a clear idea of the relevant optimality criterion. However, in many cases it is not clear from the outset what the relevant requirements / optimality criteria are. One way to deal with such a situation is to investigate the problems that would result from replacing the traits in question by the alternative traits: what problems would an organism encounter if it had the alternative traits instead of the traits in question and how do these problems relate to survival and reproduction. A typical example of such an explanation is Wehner & Bernard's (1993) explanation of photoreceptor twist in bees. In 1975 Rüdiger Wehner, Esther Geiger and Gary Bernard reported that the majority of the light-sensitive cells in a bee's eye are twisted along their length, just like a cork screw. Initially, this claim was met with disbelief. It was suspected to be an artefact of the method of preparation. However, in later years the researchers were able to establish the existence of the twist beyond any reasonable doubt. In their 1993 paper Wehner & Bernard address the question why$_2$ these cells are twisted. They show that this twist "is *necessary* for reliable encoding of information about color" (p. 4132, emphasis mine). If the cells were not twisted bees would experience a psychedelic world of ever changing colours, in which it would be difficult to impossible to find food.

Insect eyes are made up of multiple facets. Beneath each facet there is a rod-shaped light receptor, the rhabdom. Each rhabdom is composed of eight photoreceptor cells. The photoreceptor cells contain a light sensitive pigment. Due to differences in the pigment they contain, the photoreceptor cells of bees fall into different types, each of which is most sensitive to a distinct part of the spectrum. That is, cells of different types respond differently to different wavelengths. There are three types with a maximum sensitivity in, respectively, the ultraviolet, blue, and green part of the spectrum. These differences form the basis of colour vision in bees. The light sensitive pigments of all insects are stacked in an ordered array of microvilli at the edge of the light-sensitive cells. In a straight rhabdom all the microvilli of a certain photoreceptor cell are oriented in the same direction. This arrangement acts as a polarization filter. As a result the response of the different light-sensitive cells in a straight rhabdom depends not only on the wavelength but also on the angle of polarization of the incoming light. With respect to microvillar orientation there are two types. One is sensitive to light that is polarized in the dorso-ventral ("vertical") direction, the other to light that is polarized in the lateral ("vertical") direction.

In real bees most of the rhabdoms in the compound eye are twisted; straight rhabdoms are limited to the dorsal rim. To explain the twist Wehner and Bernard envisage a hypothetical bee in which all the rhabdoms are straight. The sensitivity to polarization angle would create serious difficulties for such bees. Light reflected from the waxy surfaces of plant is polarized. The direction of polarization of light reflected by a particular leaf depends on the angle between the source of light and the plane of the leaf. The angle of polarization as it is perceived by the bee in its turn depends on the direction of polarization of the light and on the line of sight. As a result, the hypothetical "straight only" bee would perceive a change of "colour" whenever it changes its direction of flight. The authors computed the sensitivity of the different types of straight and twisted photoreceptor cells as a function of wavelength. They did so for horizontally and vertically polarized light. In addition they measured the state of polarization of light reflected from plant surfaces. The measurements and calculations show that the perceived colour of the vegetation would change dramatically with the direction of illumination and the bee's line of sight. As a result of this it would be nearly impossible for the hypothetical bee to recognize and localize its food resources (flowers):

> For example, when zigzagging over a meadow, with all its differently inclined surfaces of leaves, the bee would experience pointillistic fireworks of false colors that would make in difficult to impossible to detect the real color of the flowers (Wehner & Bernard 1993: 4134).

The authors refer to this problem of their hypothetical bee as the "false-colour problem". (I think this is a rather unfortunate label: the problem is not so much that the colours are false, whatever that may mean, but rather that the perceived “colour” is not independent of the position of the bee and the direction of the incoming light). In a real bee this problem does not arise as the photoreceptor twist eliminates the sensitivity to polarization angle (as the authors demonstrate by means of calculation). In other words:

> The bee’s solution to the false-color problem is to get rid of the polarization sensitivity of its eyes by twisting its photoreceptors (Wehner & Bernard 1993: 4134).

Hence, the authors explain why most of the rhabdoms in the compound eye of bees are twisted by pointing to four factors, namely (1) the fact that differences in sensitivity of photoreceptor cells play an important causal role in the way bees process visual information (“colour” vision), (2) the fact that bees recognize and localize their food-resources (flowers) by colour, (3) the fact that light-sensitive pigments are stacked in an order array of microvilli, (4) the fact that light reflected by waxy plant surfaces is polarized. They argue that the presence of these factors would create a problem for a hypothetical organism in which the trait in question (photoreceptor twist) were absent and that the trait in question solves this problem (see fig. 8.2).

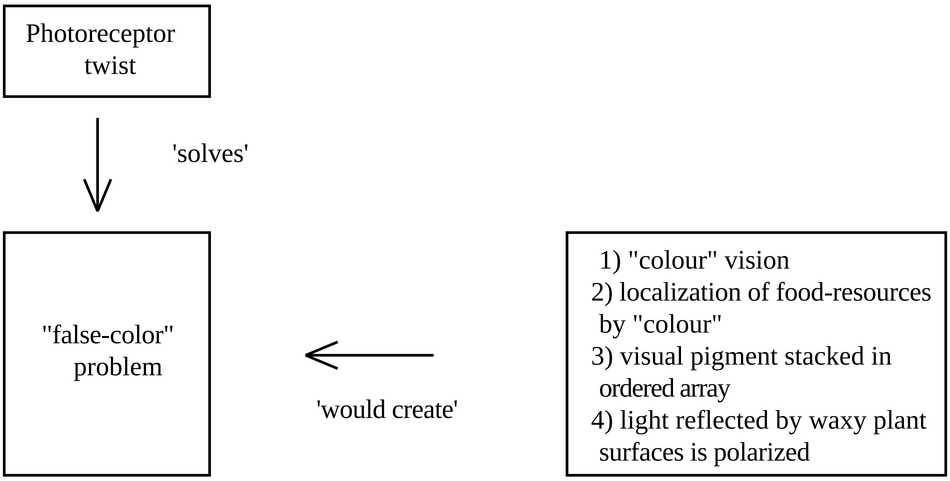

fig 8.2 photoreceptor twist

The problem consists of a series of “unwanted” (p. 4134) effects (fig 8.3). These effects are unwanted because they result in the death of the hypothetical “straight only” bee. In straight rhabdoms, the response of a certain photoreceptor cell depends not only on the wavelength of the incoming light but, due to the manner of pigment stacking (3), also on its polarization angle. Light reflected by the vegetation is polarized (4). This (3+4) means, that the “colours” perceived by a hypothetical bee with only straight rhabdoms would depend on the position of the bee and the direction of the incoming light. This would make it impossible for that bee to recognize and localize flowers by “colour”. Since, bees depend on “colour” to recognize and localize flowers (1/2) the hypothetical bee would starve to death. Twisted photoreceptors are not sensitive to polarization angle and, hence, the problem is not generated in a real bee.

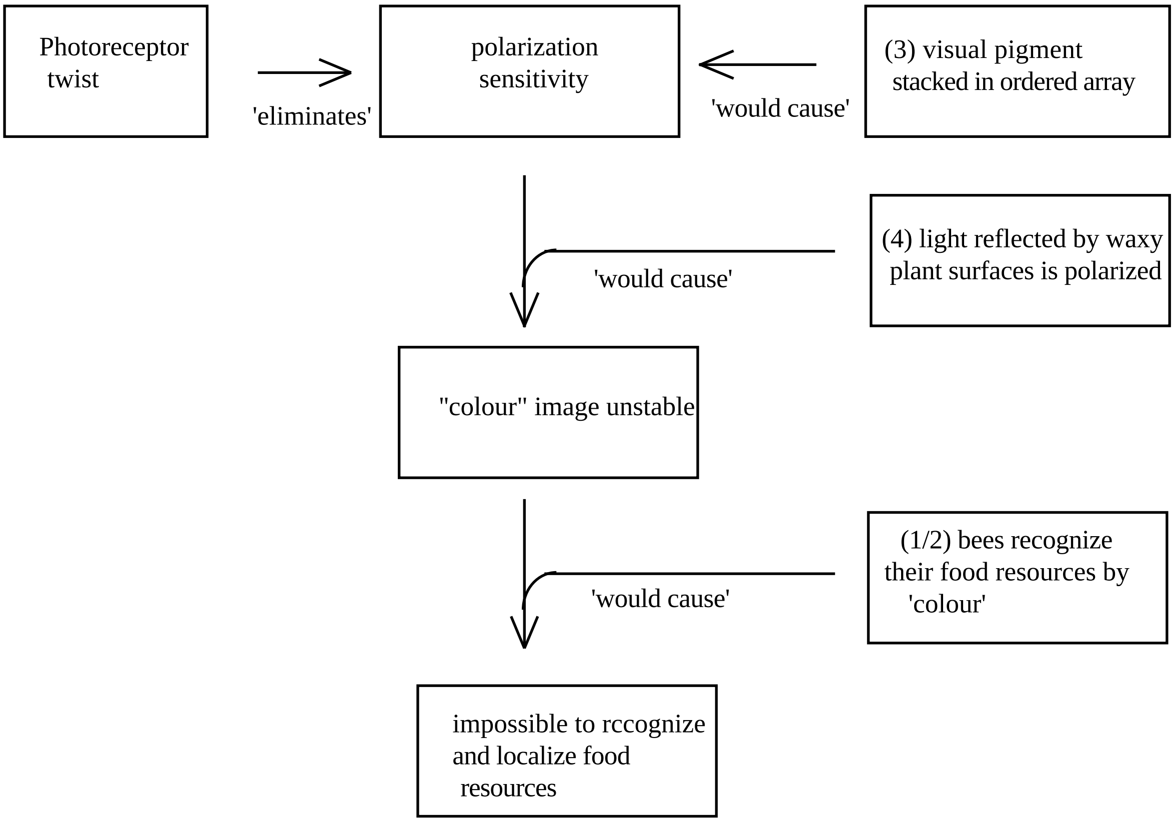

Fig 8.3: The false colour problem and its solution

Note that this explanation is easily converted into one that shows how a certain requirement is implemented (see fig. 8.4). The principle requirement is that given the bee’s feeding habits and the environment of its food resources, the bee’s mechanism of “colour vision” should enable the bee to recognize and localize flowers by sight against a background of green leaves. Given the fact that light reflected by plant leaves is polarized, this is possible if bees distinguish “colour” on the basis of wavelength, but not if “colour” depends on polarization angle. (Note at this point that in addition to explaining the photoreceptor twist the authors explain why bees distinguish “colours” on the basis of wavelength rather than on polarization angle. They do so by showing that wavelength-colours fit the requirement and polarization-colours do not.) Hence, the bee needs to get rid of any determination of “colour” by polarization angle. Given the arrangement of visual pigments a bee would not meet this requirement if all its rhabdoms were straight, but the twist solves this problem, and, hence, satisfies the need to get rid of polarization. The authors summarize their argument in the conclusion that the twist is a “necessary requirement” for recognizing and localizing flowers against a background of green leaves. It will be clear from my account that this conclusion is but a pale shadow of what they have done, namely showing how the twist is situated into a network of needs and requirements created by the other traits of the bee and the environment in which it lives.

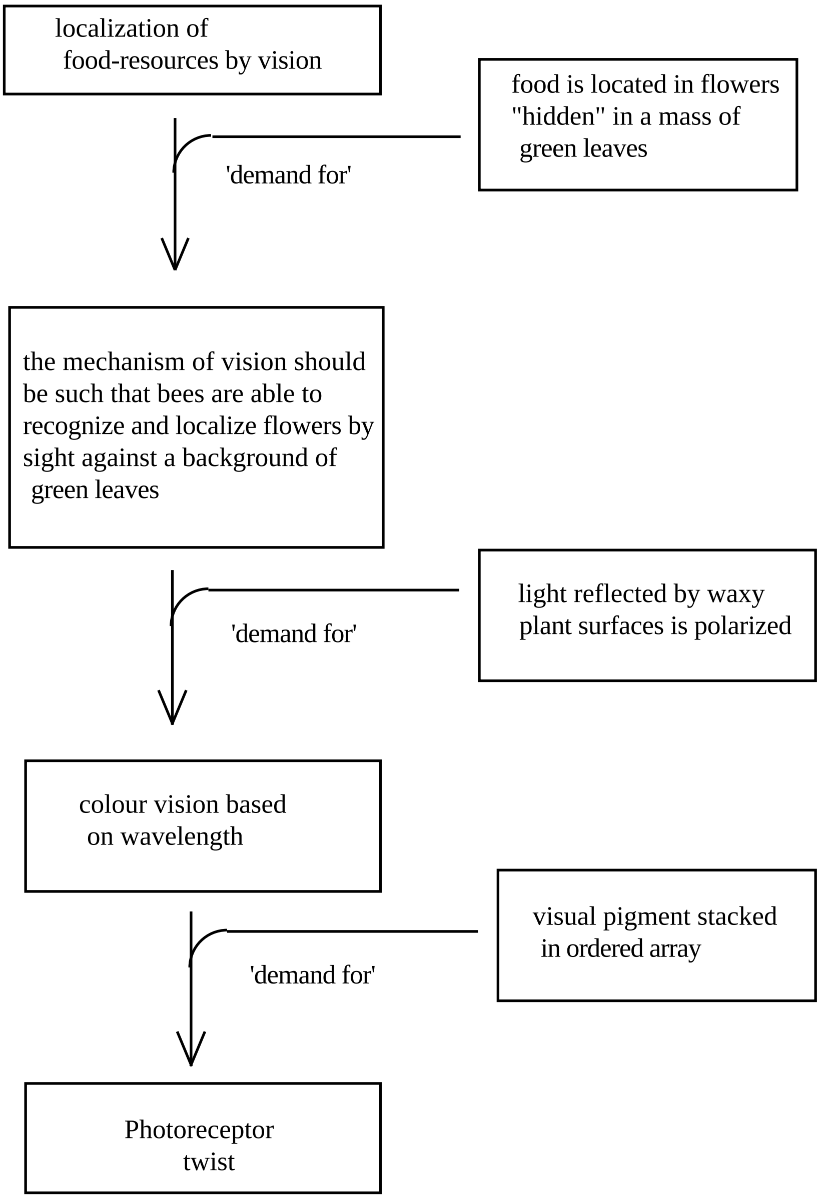

Fig 8.3 Photoreceptor twist

Egg shell removal

In the examples above the explanation focuses on one trait (the tendency of large mammals to change gait at high speeds, respectively the twist in the photoreceptors of bees). If one wants to explain complex structures or behaviours and one has only a vague idea of what the relevant alternate traits, requirements, and conditions are the following strategy is often used:

1) identify a complex task (function$_2$) in which the item or behaviour the structure of which is to be explained takes part
2) describe a simple implementation to perform this task
3) explain why this implementation has problems in the conditions in which the organisms in question live
4) describe a more complex implementation which solves this problem
5) repeat step (3) and (4) until one has an implementation similar to the structure or behaviour in question.

One of the best examples of this strategy is Van der Stelt's (1968) explanation of the arrangement of the muscle-fibres in sharks. Another good example is Langman's (1989) explanation of the vertebrate immune system. These examples are too complex to be discussed here. Instead, I will return to an example I have already discussed and show how this example fits into the third explanatory strategy. This example is the explanation of Tinbergen and his students (1962) of why many birds remove the empty egg shell after the chick has hatched. I will add details I have not mentioned before.

Tinbergen c.s. seek to explain the egg shell removal behaviour of the black headed gull. As many birds, black headed gulls remove the empty egg shell after the chick has hatched, but in contrast to waders such as the ringed plover and the oystercatcher they wait for an hour or two before they before removing the empty shell. Tinbergen c.s. start with the hypothesis that the egg-shell removal behaviour has a causal role in protecting the eggs against predators (step 1). As a first implementation of this task (protecting the eggs against predators) they envisage eggs which are camouflaged by their colour pattern (step 2). Their experiments show that bird predators find chicken eggs as easily when they are white as when they are painted like the eggs of black headed gulls (step 3). Perhaps, it is not only the colour of the eggs but also their size which plays a causal role in camouflage (step 4). To the surprise of the research team their experiments showed that carrion crows and herring gulls find the eggs of black headed gulls that are painted white almost as easily as natural eggs (step 3 repeated). In nature the eggs of black headed gulls are covered with grass and it turned out that natural eggs covered by grass are found less easily than covered eggs which are painted white (step 4 repeated). Next, the team showed that if there is an empty egg shell near the nest, the eggs are found more easily (step 3, repeated again) and that this problem is solved if the empty shells are carried away (step 4 repeated). This explains the removal behaviour but not the two hour delay. To explain the delay the team points out that in the case of colony breeders such as the black headed gulls the removal behaviour has an important disadvantage beside the advantage mentioned above. After hatching, it takes the chick a few hours to dry. In any colony of black-headed gulls there are some individuals who prey selectively on nearly hatched eggs and wet chicks. They take the chick when the parents leave the nest to attack predators or to remove the egg shell (step 3, again). As dry chicks are left alone, this problem is solved by delaying the removal for an hour or two (until the chick is dry) (step 4 again). Waders do not live in colonies and their bills aren't fit for eating chicks. Which explains the lack of a delay in their case.

8.4.2 Relation between design explanations and capacity explanations

Although capacity explanations and design explanations are to be distinguished carefully, they complement each other well. My claim is that one of the basic interests of functional biologists is to explain how the parts and processes of an organism hang together with each other and with the environment in which the organism lives. In exploring that network of interdependencies they use two main entries. One is to ask the type (4b) question "why$_2$ do such and such organisms have a certain element or perform a certain activity?", the other is to ask the type (3) question "how do such and such organisms manage to perform such and such task"? The type (4b) question is answered by means of a design explanation. Such an explanation typically starts with the attribution of a causal role in a complex activity or capacity to the element or activity to be explained. Such an attribution can be used to explain that complex activity or capacity by means of a capacity explanation. The type (3) question is answered by means of a capacity explanation. Capacity explanations attribute causal roles to the parts and subparts involved in that task. Such attributions can be used to explain the character of the parts or subparts in a design explanation. In short, answers to a type (4a) question can often be used in answering a type (3) question and the other way round. For that reason much research in biology deals with two questions at once. A nice example of such a "double-focus" approach is Eliott, Tait and Briscoe's (1993) study of the function of the crural glands of velvet worms. Velvet worms are the only members of one of the minor phyla of the animal kingdom: the onychophora. They are of considerable interest in evolutionary studies because they have characteristics in common with both the annelids and the arthropods. On the one hand the authors address the type (3) question "how conspecifics locate and recognize each other as mates" (p. 1). This question arises because of the habitat and distribution of the velvet worms: "Onychophorans are usually sparsely and patchy distributed in the dark humid crevices within rotten logs, under stones, and in leaf litter soil. Furthermore, sympatry of up to three species has been identified within the same habitat" (p. 1). The authors argue that visual and acoustic communication is improbable. The fact that the surface of the body of velvet worms is well supplied with chemoreceptors suggests that one has to look for communication by means of pheromones. On the other hand, the authors raise the type (4) question why the onychophorans have crural glands (exocrine glands that open on the ventral surface at the base of the legs). Their restriction to males suggest a sexual function. The authors were able to extract a secretion from the crural glands of males of a certain species and they show that this secretion attracts females of the same species. They conclude that their experiments establish "the function of the crural gland [in individuals of that species] as a female sex attractant" (p. 7). They add that "the role of pheromones for communication in onychophorans is clearly of adaptive significance considering their sparse and disjunctive distribution and the cryptic lifestyle characteristic of the group" (p. 8).

8.4.3 Conclusion

There are two kinds of design explanations. One kind is concerned with the type (4a) question why it is useful to individuals of certain species to have a certain item or to perform a certain activity or behaviour. They answer this question by, first, identifying a causal role of the item or activity in question and, next, showing that in the conditions that apply to the organism in question the performance of that role is useful to those organisms. The other kind of explanation addresses the type (4b) question why a certain item or behaviour has the character it has. They answer this question by, first, identifying a causal role of that item or behaviour and, next, showing that in the conditions that apply to the organism in question that causal role is better performed by an item that has the character to be explained than by an item with some other conceivable character. The conditions to which a design explanation appeals are other traits of the organisms in question and the state of the environment in which they live. This means that design explanations are concerned with relations at the individual level, just as physiological and developmental explanations. However, whereas physiological and developmental explanations are concerned with causal relations, design explanations are concerned with functional interdependencies. The main relations of functional interdependency are needs and demands. Roughly spoken, a trait is needed (required) if its presence is at least an INUS condition for an organisms to survive and reproduce. Roughly spoken, something (*B*) demands for something else (*A*) if its (*B*'s) presence is an INUS-condition for the need for that something else (*A*). Design explanations show how the different traits of an organism hang together in terms of how the different items satisfy demands imposed on them by the way in which the organism is built, the way it behaves, the way it works and the conditions of the environment in which it lives. In doing so they reveal the structure of functional interdependencies in the living world. That's how design explanations are explanatory.