# Chapter 3: Biologists about function

## 3.1 Introduction

Biologists have written surprisingly little on the notion of ‘function’. Although they often investigate functions they seldom delve into the question what it is to be a function (at least not in writing). The two main discussions of ‘function’ in morphology are still those of Bock and Von Wahlert (1965) and of Dullemeijer (1974). Other important discussion can be found in Zweers (1979) The main discussion of the notion of function in ethology is that of Tinbergen (1963).

Table 3.1: how different morphologists use certain words related to form and function.

| | Item | Form | Activity | Role | Survival value |
|---|---|---|---|---|---|
| Bock & Von Wahlert (1965), Bock (1980) | feature | form | function | biological role | |
| Dullemeijer (1974) | element | form | (potential) action, activity | meaning, purpose, role, significance | |
| Zweers (1979) | element / (sub)system | structure | action | role (function, meaning) | |
| Lauder (1986, 1990) | component | structure | function (morphology) | function (ethology) | |

## 3.2 Bock and Von Wahlert (1965)

The single most important attempt to clear up the notion of ‘function’ in morphology is made by Walter Bock and Gerd von Wahlert in their “Adaptation and the form-function complex” (1965). In this paper they contend that the term ‘function’ has two different meanings, namely ‘what it does’ and ‘what it is used for’. They propose to restrict the meaning of ‘function’ to the first meaning and coin the expression ‘biological role’ for the second. Bock & Von Wahlert are impressed by the linguistic turn in philosophy and they propose to make the distinction between function (what an item does) and biological role (how it is used) in terms of the kind of predicates involved in statements describing an organism. In their view, the difference between what an item does (function) and how it is used (biological role) is a difference of whether or not the predicates used to describe the function or role refer to the environment or not. (Bock & Von Wahlert do not explain what it is for a predicate to refer to the environment or not, but I take it that they mean that the definition of that predicate refers to the environment.) Biological roles are, by definition, the activities of organism described in terms of predicates that refer to the environment (p. 278). Predicates that do not refer to the environment describe forms or functions. ‘Form’ refers to “the class of predicates of material composition and the arrangement, shape or appearance of these materials, provided that these predicates do not mention any reference to the normal environment of the organism” (p. 272). ‘Function’ refers to “that class of predicates which include all physical and chemical properties arising from its form [...] including all properties arising from increasing levels of organization, provided that these predicates do not mention any reference to the environment of the organism” (p. 274). Bock & Von Wahlert emphasize that a certain function in one animal may have many different roles and that the same function may have different roles in animals of different species:

> For example, the legs of a rabbit have the function of locomotion—either walking, hopping, or running—but the biological roles of this [activity][1] may be to escape from a predator, to move toward a source of food, to move to a favorable habitat, to move about in search of a mate, and so forth. The legs of a fox also have the function of locomotion, although the details of the form and the function of the fox leg differ greatly from the rabbit leg. Yet some of the biological roles are quite different in the fox and in the rabbit. One role of the leg in the fox would be to catch its prey when it is chasing the rabbit in which the role would be to escape from its predator (Bock & von Wahlert 1965: 279).

According to Bock & Von Wahlert the distinction between function (what a certain item does) and biological role (how it is used) is important for two reasons. First, they want to emphasize that it is not sufficient to study an organism’s capacities in order to know how those capacities are used by the organism. As an example they recall Bock’s mistake in inferring the use of the mucus gland of the gray jay (*Perisoreus canadensis*):

> Bock (1961) suggested that the biological role of the large mucus glands of the gray jays was to coat the tongue with a glue-like material which would allow the bird to obtain food from crevices in the bark of trees and thus is similar to the biological role of the large mucus glands in some woodpeckers. Dow (1965), however, has shown, by observations of these birds in captivity and in the wild, that the mucus serves as a glue to cement food particles together into a food bolus which is then stuck to branches of trees. These food boli are a device to store food during the winter; the stored boli are found and eaten

[1] Bock & Von Wahlert use the term 'faculty', which is a combination of a form and a function$_1$.

> during stormy weather and other periods during which these jays cannot find food (Bock & von Wahlert 1965: 278/9).

Bock & Von Wahlert's second reason is related to their first: they seek to emphasize the importance of field studies to morphology.

> The function of [an item][2] may be studied and described independently of the natural environment of the organism as is done in most studies of functional anatomy (Bock & von Wahlert 1965: 274)

> Essential to the description of a biological role is the observation of the organism living naturally in its environment. The descriptive adjective "biological" stresses this fundamental property of the biological role. A biological role cannot be determined by observations made in the laboratory or under artificial conditions. (Bock & von Wahlert 1965: 278)

Functions in their sense are the things that can be studied in the laboratory, biological roles should be studied in the wild. Bock has repeated this concern several times (1980, 1990). He also urges the need for developing and funding the morphological study of the relation between organisms and environment (ecomorphology) on the ground that with the extensive destruction of natural environments this study may soon become impossible.

In emphasizing the distinction between "what an item does" and "what an item is used for" Bock & Von Wahlert make an important point that should be taken into account in any account of function. In my account this distinction appears as the distinction between on the one hand an item's activities and capacities (function$_1$) and on the other hand its causal roles (function$_2$). However, the way in which Bock & Von Wahlert seek to make this distinction has several problems. As I said, they seek to make this distinction in terms of whether or not the predicates involved refer to the organism's environment. This does not work for reasons that will become clear shortly. Moreover, their association of this distinctions with the distinction between what can be studied in the laboratory and what should be studied in the field does not work either.

A first problem is that in stating how an item is used one often does not refer to the organism's environment. In section 2.1.1 I discussed the circulation of the blood (example 2.1). This is an activity (something an item does) that is used by the organism for, among other things, the transport of oxygen, nutrients, wastes and heat. In saying that the circulatory system is used to transport oxygen, nutrients, wastes and heat one does not refer to the environment of the organism. Bock & Von Wahlert themselves use the term 'role' several times in this sense:

> Bony skeletal elements possess great strength against compression, tensile and shearing stresses which allow their *role* as support of the body, points of attachment for muscles and mechanical protection of vital organs (Bock & von Wahlert 1965: 275, italics mine).

[2] Bock and Von Wahlert use the term 'feature'

> Collagenous fibered tendons and ligaments possess great strength against tensile stresses and are highly non-compliant (not stretching), but they have no strength against compression or shearing forces which allows their *roles* as the intermediate structure between muscles and bones and the ties between individual bones (Bock & von Wahlert 1965: 275, italics mine).

This way of talking suggests a tripartion along the lines I have set out in chapter 2.

A second problem is that many predicates that tell us what an item does do refer to the environment of the organism. Consider for instance Bock & Von Wahlert's contrast between the "function" of locomotion and the "biological role" of escaping from a predator (see the first quote in this section). If locomotion is defined as the ability to move or as the act of moving from one place to another it clearly refers to the organism's environment. Hence, the presence or absence of reference to the organism's environment does not work to make the distinction between locomotion as a predicate that states what an item does and escaping from a predator as a predicate that states how that item is used. Other "function" predicates that clearly refer to the environment are camouflage (which may have the "biological role" of escaping from predators, as in the case of the peppered moth, or of hiding oneself to approach a potential prey as is the case with the stripes of the tiger) and insulation. Moreover, most if not all "functions" (capacities) depend on the environment. A bird's capacity to fly, for instance, depends on atmospheric pressure, drag, gravity and so on. The capacity to circulate oxygen depends on atmospheric pressure, the partial pressure of oxygen in the environment (whether it be air or water) and so on. Of course, Bock & Von Wahlert are themselves well aware that "function" depends on the environment, but they do not seem to realize that this blurs the way in which they make the distinction between "what an item does" and "how that item is used".

As I said, Bock & Von Wahlert define the distinction between "what an item does" and "how that item is used" in terms of an internal / environmental distinction. In doing so they associate the distinction between "what an item does" (its function) and "how that item is used" (its biological role) with a distinction between what can and what cannot be studied in the laboratory. Because descriptions of "functions" do not refer to the environment "functions" might be studied in the laboratory and because descriptions of "biological roles" do refer to the environment these should be studied in the wild. In emphasizing the need for field studies Bock & Von Wahlert have an important point. However (and this is the third problem of their approach) the distinction between the different kind of functions does not run along the same lines as the distinction of what can be studied in the laboratory and what should be studied in the wild. How much of the role / survival value can be studied in the lab depends on how much of the natural conditions are carried over to the lab. For a whale or a bird this will be very difficult. But what about a flatworm or a gastropod? Furthermore, some functional$_1$ data (such as the running speed of a leopard when chasing a prey) could be obtained from field studies only.

In my account the distinction between kinds of predicates is derived from a prior distinction of kinds of functions, rather than the other way round. The distinction between predicates like ‘locomotion’ and ‘camouflage’ on the one hand and predicates like ‘escaping from predators’ and ‘approaching a prey’ on the other hand, is not that the last refer to the environment and the first do not, but rather that the first refer to an observable process or state ($function_1$) and the second to a certain role in maintaining a capacity, process or state ($function_2$). By labelling a certain behaviour as ‘escaping from a predator’ one points out a role of that behaviour (for example in the survival of the organism), by labelling the same behaviour as ‘locomotion’ one describes the process but does not ascribe a role to it. One might construct role predicates from descriptive predicates by prefixing the descriptive predicates with something like ‘has a role in’, ‘takes part in’ or ‘participates in’, e.g. ‘participates in locomotion’. As a result descriptive predicates are used both in sentences that describe or label activities and capacities and in sentences that ascribe roles (in more or less detail). For example, if someone states that “rabbits have three types of locomotion: walking, hopping and running” the predicates ‘walking’, ‘hopping’ and ‘running’ are used to describe the activity of locomotion. However, the sentence “the legs have the function of locomotion” does not describe a certain activity but rather states that certain items (the legs) take part in the complex activity of locomotion. For the sake of clarity it would be better to use constructions like “the legs participate in the activity of locomotion” or “the legs have a role in locomotion”.

## 3.3 Dullemeijer (1974)

In his *Concepts and Approaches in Animal Morphology* Dullemeijer (1974) undertakes an investigation of the methodological and conceptual principles of functional animal morphology. This monograph is most interesting for my purposes. It shows that my account of functional explanation is close to the ideas embraced by working biologists. On the other hand my account improves on that of Dullemeijer. According to Dullemeijer the principle object of functional morphology is the relation between form and function. Form is defined as the spatial extension of an item. In the case of bone (which is Dullemeijer’s main example) the main aspects of form are: its presence or absence, its position, its size, its shape, its structure and its composition. Dullemeijer’s account of function, is less clear. According to him one should distinguish three aspects of function:

> the concept of function denotes action, biological significance and the encompassing conception of relation (Dullemeijer 1974: 49).

Action (also called “activity”) is defined as any change of form (including a change in position). Biological significance (also called ‘meaning’, ‘purpose’ and ‘role’) is the way in which an item serves the maintenance of the organism, that is its role in the animal's physiology. "The encompassing concept of relation" refers to the way in which the several items of an organism are related to each other in the organism's physiology. According to Dullemeijer:

> [An item that has a function][3] forms an essential part, a member of that existing organism, because of its relation to other parts. Function here is equivalent to the relation of one element to another (Dullemeijer 1974: 48).

This relation is constitutive of the item that has the function.

> [Items][4] must not be treated as things having properties, but as phenomena that exist consequent on relations (Dullemeijer 1974: 48).

In other words:

> function equals relation (Dullemeijer 1974: 48).

For a start, Dullemeijer considers "a statement on a relatively simple relation between form and function": "aquatic vertebrates have fins to move or to propel" (p. 52).[5] He observes that this statement is unsatisfactory:

> the simple statement on the aquatic vertebrates is unsatisfactory [..]. This discontent is not felt because of its simplicity, but because of a shortage of information to gain an insight into the *relation* between propulsion and fins [emphasis in original] (Dullemeijer 1974: 53).

The relation between form and function can be written symbolically as a mathematical function:

$$S = f\,(F)$$

where the $S$ (of structure) stands for a form, $F$ for a function and $f$ for the relation of form and function (p. 54).

According to Dullemeijer there are two main approaches to determine $f$: "the comparative or inductive method" and "the non-comparative or deductive method" (p. 55). The comparative method correlates the form of a certain item with the function(s) it performs in the different taxa. The deductive method starts with an analysis of the requirements imposed on an item by the function(s) it performs. Next, a theoretical form (a so-called "model") is deduced that fits these requirements and this theoretical form is compared to the actual one.

The first task of functional morphology is to describe the relation between function and form. According to Dullemeijer this relation is of "an acausal character":

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[3]Dullemeijer says at this point "a structure, an element that has a function".

[4]Dullemeijer: "elements"

[5]Note that this statement can be converted into the philosopher's standard form: "the function of fins in aquatic vertebrates is to move or to propel".

> It is a relation of correlation instead of causality, because the relation does not contain a time parameter (Dullemeijer 1974: 65).

He continues:

> After having established that such a relation does occur, the following questions arise: how is the relation to be explained in terms of underlying mechanisms or factors, how in terms of the biological role or meaning, and how has it evolved in the ontogeny and evolution (Dullemeijer 1974: 65).

In the course of the book it becomes clear that in Dullemeijer's view the relation that should be used to explain the relation of form and function (e.g. the relation between propulsion and fins) in terms of their role is that of "demand". According to Dullemeijer (p. 79) "activities are demands upon form" and it is by appeal to those demands that it becomes possible to explain the relation between form and function in terms of its role.

Dullemeijer lumps too many things together, but under the woolly language he makes some important points. Let me try to clear up his account by making a number of distinctions. Instead of speaking of "*the* relation of form and function" it is important to distinguish between several kinds of form-function relations. Firstly, there is the relation of performing a certain activity ($function_1$), e.g. the heart beats. This is a relation between an item (not: a form) (e.g. the heart) and an activity (beating). Secondly, there is the relation of having a certain causal role ($function_2$) e.g. teleost fish use their extremities[6] to propel themselves in water. This is a relation between an item (not: form) (e.g. the extremities of teleost fish) and a causal role (e.g. to propel) in individual organisms of a certain taxon. Thirdly, there is the factual correlation of the form of an item and the functions (activities and roles) it performs in different groups of organisms (e.g. all aquatic vertebrates use fins for propagating themselves). This relation is established by comparison. Fourthly, there are the causal relations that explain how the item is able to perform its functions (roles and activities) in a certain environment, e.g. how thrust is generated by beating the fins in water. Fifthly, there is the relation of the demands imposed on the form of an item by the combination of the functions (activity or role) that item performs and the environment(s) in which the organism lives. This relation can be used to explain both the form of an item (not: to explain the relation of form and function, as Dullemeijer says) in a certain individual by appeal to the function of that item and the correlation of form and function in different groups of animals (an example would be a physical explanation of why in water propagation by means of fins works better than propagation by legs). Such explanations proceed by showing that only certain forms fit the demands (requirements) imposed on it by

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[6] I use the word "extremities" at this point because the word "fin" is ambiguous: it is used to denote both a certain item (the extremities of fishes) and the form that item takes in fishes (fins as opposed to legs). I'll return to this issue in chapter 4.

these functions. These explanations are the kind of explanations that are traditionally called ‘functional explanations’ and which I have called design explanations (i.e. the explanations ad. (3) of section 2.3).

Given these different kind of relations it is clear that one should distinguish the following activities: (1) determining which functions a certain item performs, (2) determining a correlation between form and function in different groups of animals, (3) determining which demands the functions of an item impose on the items that perform those functions, (4) explaining how a certain item performs a certain function, (5) explaining why an item is built the way it is built by appeal to the demands imposed on that item by the functions it performs, and (6) explaining a correlation between form and function in different groups of animals by appeal to the demands imposed on the items that perform those functions. Dullemeijer is himself more or less aware of these distinctions. However, he fails to state them explicitly and this confuses his account. For example, as I said a few paragraphs earlier, according to Dullemeijer there are two main approaches to determine the relation between form and function: inductive or comparative and deductive or non-comparative (p. 55). This is confused both because the comparative method and the deductive method are concerned with different kind of form-function relations (the comparative method is concerned with the factual correlation of the form of an item and the functions it performs in different groups of organisms and the deductive method is concerned with the relation of demand) and because these two relation do not exhaust the possible form-function relations (there are also the relation that a certain item performs a certain function and the relation how it performs that function). Dullemeijer is himself aware of the fact that the comparative method and the deductive method are concerned with different relations and activities where he says that

> the established relation [established by comparison] can be taken as an explanation. But one needs a deduction to explain the relation (Dullemeijer 1974: 77).

This is a confused way of saying that the comparative method establishes (but does not explain) a correlation between form and function (activity 2), and that we need the deductive method to explain this correlation (activity 3 and 5).

## 3.4 Zweers (1979)

According to Zweers (1979) morphologists should view their object (organisms and their parts) as systems consisting of subsystems. Morphology is basically concerned with the question “why is a system built the way it is, and why not different?” This question has three aspects. Firstly, one should ask “how is the system built” or “how does it look like”. Next, one should raise the question “how does the system work, i.e. function?”. Finally, one should ask “as a result of what evolutionary and developmental processes did the system arrive at its present state?” (p. 422). Zweers’s account could be improved by making a clear distinction between “functional explanations” and answers to the question “how does it work”. The first explain why a system (item) is built the way it is in terms of its roles in a larger system. The latter explain how the system (item) is able to perform a certain activity ($\text{function}_1$) in terms of an underlying mechanism. As I said in section 2.3.4 explanations of the latter kind attribute roles ($\text{functions}_2$) to the parts of the system the activity of which is explained.

Zweers contrasts “structure” (form) parameters with “action” ($\text{function}_1$) parameters:

> There are two categories of parameters which have been used in functional morphology to describe the investigated object. These categories are the structure parameters and the action parameters. The structure parameters are distance, position, size, shape, hardness, volume, mass, weight, colour, etc. The action parameters and their derivatives form a long series: movement, velocity, acceleration, vibration, force, momentum, work, power, potential and kinetic energy, friction, elasticity, viscosity, stress, strain, tensile strength, compressive strength, impact strength, heat parameters, conductivity, electric activity other electric parameters, sound, etc. (Zweers 1979: 423).

The term “role” gets its meaning in the context of systems of subsystems:

> The term “role” is primarily defined as the service of any [item][7] at some level of organization for a higher level of organization (Zweers 1979: 423).

or:

> The terms role, biological role, biological function, biological meaning and function are taken to be equivalent. We prefer the use of the term “role”. A role is defined as the service of a member for the system(s) to which the member belongs (Zweers 1979: 423).

Hence, a system is characterized by three types of parameters: structure, action and role.

According to Zweers the difference between actions and roles is relative to the level of investigation:

> If we take a particular structure or action parameter of a member (*i.e.* subsystem), this parameter can become a role parameter if the member is taken as the system being studied, without the member’s relation with the higher system. Thus the shortening of the lingual muscle will be considered as an action of the lingual system, but the same shortening is considered to be a role as soon as the lingual muscle itself is taken as the system selected for investigation apart from and instead of the lingual system (Zweers 1979: 424)

[7] Zweers uses the term 'element'.

In this quote, Zweers depicts the shortening of the lingual muscle as an action of the lingual system, that becomes a role of the lingual muscle if the latter is taken as the item under study. In other words: according to Zweers the shortening of the muscle is seen as a role if it serves as the activity to be explained in an explanation of how a certain item (the lingual muscle) works, and the shortening of the muscle is seen as an action if it is used to explain how a system (the lingual system) that contains that item (the lingual muscle) performs its role. In my account, whether or not a certain change is called an activity (function$_1$) or role (function$_2$) does not depend on the way it is used in explanations. The shortening of a muscle is an activity (function$_1$), because in saying that a muscle shortens one does not say much about its effect on a larger system. This activity can serve as the activity to be explained in an explanation of how the lingual muscle works. It can also be used to explain the activity of a system of which it is a part. For instance, it might be used to explain how the lingual system works. As part of the latter explanation one will have to attribute a role to the muscle and its activity, for instance to move a certain bone, in a certain direction.

## 3.5 Tinbergen (1963)

The classical treatment of function as survival value in biology is Tinbergen’s “On aims and methods of Ethology” (1963). The paper is a classic in ethology, but it has almost been ignored in the philosophy of biology. As far as I know, Horan (1989) is the only philosophical paper that discusses Tinbergen’s article. Tinbergen distinguishes four problems of biology: causation, survival value (or function), ontogeny and evolution (p. 411). He observes (p. 417) that many biologists in his time are suspicious of explanations in terms of survival value. They hold that exact, experimental methods do not apply to the study of survival and that the assessment of survival value must, therefore, detoriate into unscientific guesswork. Tinbergen argues that this suspicion is undeserved. He appears to have three arguments. First, he lists many examples of studies demonstrating survival value as good as anyone could wish. His other two arguments are of a more philosophical nature: they concern the nature of the relation under investigation and the existence of a reliable method to demonstrate that relation. Tinbergen emphasizes that both physiology and the study of survival value are concerned with cause-effect relationships.

> The only difference is that the physiologists looks back in time, whereas the student of survival value, so-to-speak, looks “forward in time”; he follows events after the observable process has occurred (Tinbergen 1963: 418).

In Tinbergen’s view, this difference between the study of physiological causes and of survival value is, just “an accident of human perception”. In the case of physiological studies, due to our constitution, the effect is the thing that is easily observed and the cause is something to be discovered. However, in ethology the thing that is observed most easily (a certain behaviour) is the cause and the effect (its survival value) is the thing to be discovered. Tinbergen's third argument concerns the method of investigation (Actually, Tinbergen himself appears to be unaware of the difference between the two arguments, he seems to equate cause-effect relations and relations that can be observed repeatedly). He is convinced that the undeserved suspicion of the study of survival value is due "to a confusion of the study of natural selection with that of survival" (p. 418). Whereas evolutionary studies of selection deal with unique past events that cannot be observed repeatedly and, hence, can never be subjected to experimental proof, the study of survival value (like physiological and developmental studies) is concerned with a flow of events that can be observed repeatedly and which thus can be subjected to experiments. The survival value of a certain morphological or behavioural element, therefore, can be established in a reliable way:

> The method to demonstrate survival value of any attribute of an animal is to try whether or not the animal would be worse off if deprived of this attribute" (Tinbergen 1963: 419).

This is easy with morphological items but if the attribute is a behavioural pattern it is often rather difficult to create an experimental organism that lacks just the attribute to be studied. This difficulty may be overcome by systematic comparisons of the success of animals at times when they do show a certain behaviour with the success at times when they do not, and by the use of dummies, such as plastic sticklebacks.