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Towards a Methodology of Teleonomy[1]

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'The study of adaptation is not an optional preoccupation with fascinating fragments of natural history; it is the core of biological study' (PITTENDRIGH[2]).

'In any case, these [evolutionary] considerations will always remain speculative and should be left at that' (ENGELMANN[3]).

The problem of adaptation is the only one by which biology differs fundamentally from all other natural sciences[4]. It's therefore surprising to see how little this basic problem has been studied. This deplorable situation is mainly due to three reasons, as many discussions with biologists have made clear to me: 1. Because of historical reasons, the question is thought to be contaminated with Aristotelian finality. 2. The claim of the theory of natural selection to explain historical events empirically remained misunderstood and its explanatory potential went unrecognized. 3. The main reason, however, seems to be the lack of a methodology. For instance, many biologists of our days still do not know that natural selection can be investigated experimentally. Consequently I shall try to outline below some avenues of approach to study the problem of 'adaptation'. Because of lack of space, theory, questioning and methodology must necessarily remain rather unsophisticated.

In 1859 the study of the problem of adaptation received a precise foundation, when DARWIN published his theory of natural selection. For approximately 70 years its core remained a concept falsely epitomized as 'survival of the fittest' and 'struggle for survival', two well-known clichés which DARWIN had adopted from H. SPENCER (see [5]), and that still nowadays serve for an erroneous characterization of a misunderstood theory[6,7]. The theory of natural selection, as it stands since the early Thirties[8–10], describes how all those characters of an organism are selected which ensure for their owners, as opposed to other members of the species, a higher reproductive success, i.e. it implies differential survival of genotypes in a population. The theory of natural selection consequently explains the survival of *species*, and the survival of the individual only inasmuch as it serves its reproductive success. Further misunderstandings and errors, which still nowadays hamper progress of evolutionary research, will be briefly dealt with in an appendix.

One of the major drawbacks, which prevented the general acceptance of the theory by the causally oriented evolutionists, was the alleged goal-directedness of selection. This goal-directedness gave rise to the confusion with Aristotelian teleology; it was overlooked that natural selection was the cause for the development of adaptations and not a causa finalis to be rejected with good reason. In recognition of this unfortunate, semantic historical burden of the study of adaptations, PITTENDRIGH[2] coined for it the term 'teleonomy' in order to give the seemingly finalistic question of the 'what for?' of biological phenomena a strictly causal meaning. Accordingly, teleonomy thrives at the causal answer to the question of the nature and the operation of selection pressures (factors). The proposal to redefine the old term of teleology in this way[11] seems to me confusing.

Basic concepts

The identification of the responsible selection pressure which has shaped a given character of an organism is a necessary pre-requisite to unravel its function or biological significance.

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[1] Altered version of a paper read at the 3rd German Speaking Ethological Conference 1972 at Radolfzell, Bodensee (Germany, Fed. Rep.)

[2] C. S. PITTENDRIGH in *Behaviour and Evolution* (Eds. A. ROE and G. G. SIMPSON; Yale University Press, New Haven, London 1958), p. 395.

[3] F. ENGELMANN, *The Physiology of Insect Reproduction* (Pergamon Press, Oxford, New York 1970), p. 223.

[4] G. SOMMERHOFF, *Analytical Biology* (Oxford University Press, Oxford 1950).

[5] T. DOBZHANSKY in *Population Biology and Evolution* (Ed. R. C. LEWONTIN; Syracuse University Press, Syracuse, N.Y. 1970).

[6] M. EIGEN, Naturwissenschaften *58*, 465 (1971).

[7] P. SCHUSTER, Chemie in unserer Zeit *6*, 1 (1972).

[8] R. A. FISHER, *The Genetical Theory of Natural Selection* (Oxford University Press, Oxford 1930).

[9] S. WRIGHT, Am. statist. J., March Suppl. (1931), p. 201.

[10] J. B. S. HALDANE, *The Causes of Evolution* (Harper, London, New York 1932).

[11] F. AYALA, Philosophy Sci. *37*, 1 (1970).

If one looks at an adaptation at a given time one will not known anything about the speed of its evolutionary development. If, for the sake of simplicity, one leaves aside time, one can symbolize the co-action of several selection pressures simply by means of a vector symbolizing the strength and the direction of selection (Figure 1). The depth of the angle signifies the maximally attainable degree of perfection for a given adaptation. In the particular example chosen here, interaction between selection pressures was not considered. The direction of selection determines the nature of the adaptation. Given two selection factors acting in the same direction but with different strength, the answer of the adapting organism will be equally strong, irrespective of whether there are two (b) or only one (a) selective agent(s) at work, if the latter is as strong as the more effective of those working in unison; s″ cannot conceivably operate in the presence of s′ because the species cannot 'perceive' it. In general this applies only if the individuals least adapted to s′ are no longer affected by s″. This condition in turn depends on how much s′ is smaller than s″ and on the individual variability of the adaptation achieved. In case s′ would suddenly cease to operate, the adaptation coping with it would also be advantageous in coping with s″. From this follows: *An adaptation arises only through the operation of the strongest of several selection factors acting in the same direction.* This conclusion rules out the wide-spread but erroneous idea that every observed advantage would derive from the effect of selection. By contrast, one has to examine carefully whether an advantage has not been gained as a by-product of an adaptation to a stronger selective force. If, for instance both, cold and drought select a spherical shape, i.e. the most advantageous ratio of volume to surface, then approximation of a sphere would only be achieved by the stronger of two selective agents acting in the same direction.

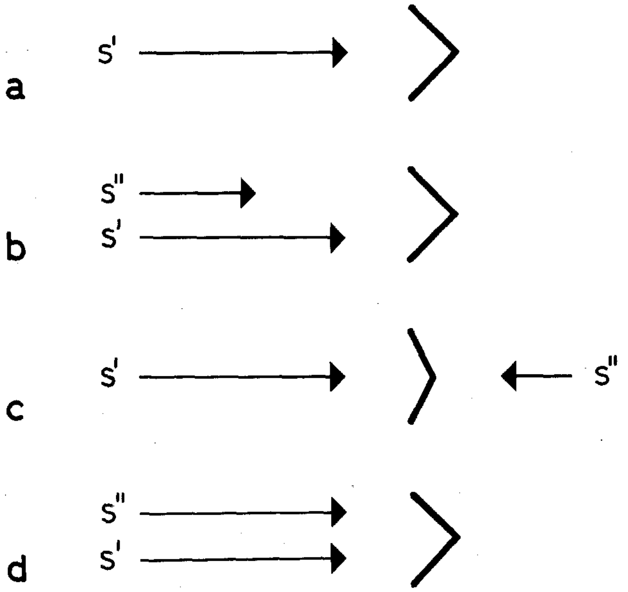

Fig. 1. Diagram illustrating the effect of one or two selection pressures upon an adaptation > in the state of maximally possible perfection. Direction and strength of the selection pressures are symbolized as vectors. For further explanation, see the text.

If two selection pressures act against each other ('counter-selection'), a comprise solution[12–14] is commonly arrived at which is capable of coping, though not perfectly, with both selective agents (c). This counter-action need not follow algebraic addition; instead selection pressures operating in different directions can interact with each other. Precise action in parallel (b) and precise counter-action (c) are but borderline cases along a scale with many possibilities of the direction of two or more selection pressures.

The effect of two equally strong selection pressures which act in the same direction upon the degree of perfection of an adaptation is as strong as any one of them alone (d). (In the latter case the adaptation would *ceteris paribus* arise more slowly than could be demonstrated by the inclusion of the time factor). Two predators with precisely identical hunting strategy effect a prey species only as strong as anyone of them: Doubling the number of individuals of one of them would replace the effect of the other one. Probably the case (d) under consideration would only be relevant for abiotic selection factors and would then occur perhaps only rarely; synecological relations, e.g. the pressure of several predators or competition with several similar species etc. would always tend to follow paradigm (b) since in no place are there two predators with identical hunting strategy and in no place, because of the competition exclusion principle by Gause, will competing species with precisely identical ecology occur.

Adaptation denotes both the evolutionary process as well as its end-product. In the following only the former meaning will apply. Adaptations may be obligatory or may be facultative, i.e. will only occur under certain environmental conditions. The most versatile 'organ' in this respect is the learning ability of animals.

Dobzhansky[5] has distinguished between the adaptedness of a population and the Darwinian fitness of the individual. The measures for both these aspects are very often correlated in one and the same population, yet there are exceptions. In the following only Darwinian fitness, as measured by reproductive success, will be discussed.

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[12] E. Mayr, Proc. XII Int. Orn. Congr., Helsinki 1958 (1960), p. 495.

[13] G. Osche, in *Handbuch der Biologie* III/2 (Ed. Bertalanffy), 817 (1966).

[14] N. Tinbergen, Proc. XIV. Int. Orn. Congr. 1966 (1967), p. 43.

Earlier attempts at defining criteria for adaptations

If one is to study adaptations, one has to recognize them. The very fact that an organism is adapted to its environment does not mean at all that it consists only of adaptations. One has to consider the possibility that there are rudiments, 'the adaptations from yesterday', as well as hidden potentials which do not offer anything on which selection could work (see below). The overall design of a phylum, commonly thought to be unaffected by reconstruction through selection and consequently denoted as non-adaptive 'ancient heritage', is actually exposed to selection as any other more recently acquired character[15].

It is to WILLIAMS[16] that we owe the first though still little formalized attempt to enumerate the following five diagnostic criteria for characters which deserve the onerous term adaptation: 1. economy, 2. sufficient precision, 3. efficiency, 4. complexity, 5. constancy, i.e. a wide-spread occurrence of the character under consideration in many species. It remains questionable whether any one of the criteria mentioned alone is sufficient. It is out of question that all of them are not neccessary for already a simple 'larger' or 'smaller' could be selected for, that is to say would not neccessitate the criterion of complexity (4.) for labelling a given structure an adaptation. Similarly constancy (5.) is as little necessary. Even if there were only one species on earth, it would be adapted to its particular environment. A more serious drawback of WILLIAMS' criteria lies in the fact that they are mainly interdependent. For instance, economy, precision and complexity are intimately related with each other (see below) and all of them are dependent upon efficiency; efficiency itself can only be measured operationally and sensefully by the selective value of a given structure (p. 1057). The *economy principle* plays a central role in these considerations. It postulates that an organism invests only as much energy into the formation of a structure as it derives profit from it. BOCK and v. WAHLERT[17,18] view the economy principle as the only and neccessary criterion of an adaptation and its development. A weakness of the economy principle is that in principle, by its logic, it appears impeccable but that in reality its quantitative verification will be difficult. If it is correct that precision requires energy, a structure or behaviour may be only inasmuch precise as the economy principle would demand. Compatible with this view, although not being a proof, is the fact that the sensitivity of sense organs exceeds the range of sensitivity which would normally be necessary for the reception of adequate stimuli[19,20] or that releasing mechanisms concordantly are 'open to one side'. Well-known examples are the epigamically effective frequency of the wingbeat of the Silverstreak (*Argynnis paphia*) upon the sexually responsive male[21], or the incubation by Oystercatchers (*Haematopus ostralegus*) of eggs which have been artificially enlarged out of all proportion[22]. The male Silverstreak responds up to 75 wing beats per sec by its nuptial flight with increasing strength the quicker the wings of the female dummy are beating, although the natural female will never have more than 8 beats per sec. These releasing mechanisms are economical because they lack a precision which they do not need. If this interpretation is correct one has to reckon with more than one selective force each time one finds a mechanism or a structure with a sharp limitation which cannot be readily explained in other ways.

One case in point is the hunting strategy of birds which is obviously dictated by the tendency to preserve energy in accordance with the economy principle. Great Tits (*Parus major*) provide their nestlings with larger caterpillars than fledged young or than if caring for themselves[23] (see also [24,25]). Obviously the parent bird behaves economically if for longer flights it selects large prey, namely when it flies back and forth to its nest; for shorter flights, namely when the fledged brood is able to follow their parents, or if hunting for self-maintenance, prey may be smaller. Moreover, adult birds visit many times in succession a segment of their territory in which they have just discovered ample prey[23] (see also [26,27]).

It is reasonable to assume that the range of validity of the economy principle can give hints to look for adaptations if a certain degree of complexity (4th criterion of WILLIAMS) is realized. The build-up of complexity doubtless requires energy, and energy will only be expended if the advantage repays. Notwithstanding the plausibility of these considerations it is extremely difficult in praxis to measure complexity. Though only intuitively applied, the criterion has already succeeded many times: After intense research one discovered finally the function of the lateral line organ of fish analyzing damming pressure[28], the pits of the pitvipers (Crotalidae) as warmth detectors[29]; after decades of effort the function of the ampullae of

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[15] A. J. CAIN, in *Viewpoints in Biology* (Eds.: J. D. CARTHY und C. L. DUDDINGTON; 1964), vol. 3, p. 36.

[16] G. C. WILLIAMS, *Adaptation and Natural Selection* (University Press, Princeton, N. Jersey 1966).

[17] W. BOCK and G. v. WAHLERT, Evolution *19*, 269 (1965).

[18] D. S. PETERS and W. F. GUTMANN, Z. zool. Systematik Evolutionsforsch. *9*, 237 (1971).

[19] E. PRIESNER, Z. vgl. Physiol. *61*, 263 (1968).

[20] K. DUMPERT, Z. vgl. Physiol. *76*, 403 (1972).

[21] D. MAGNUS, Z. Tierpsychol. *15*, 397 (1958).

[22] N. TINBERGEN, *The Study of Instinct* (Clarendon Press, Oxford 1951).

[23] T. ROYAMA, Proc. adv. Study Inst. Dynamics Numbers Population (Oosterbeek 1970), p. 344.

[24] H. LIND, Dansk orn. Foren. Tidsskr. *59*, 1 (1965).

[25] R. B. ROOT, Ecol. Monogr. *37*, 317 (1967).

[26] S. SIMONS and J. ALCOCK, Ibis *113*, 477 (1971).

[27] J. SMITH and R. DAWKINS, Anim. Behav. *19*, 695 (1971).

[28] S. DIJKGRAAF, Biol. Rev. *38*, 51 (1963).

[29] T. H. BULLOCK and F. P. J. DIECKE, J. Physiol. *134*, 47 (1956)

Lorenzini of the Elasmobranchs recently became known as being sensitive to the weak biogenic electric field of prey animals hidden in the sand[30]. At the same time these examples do show that, consciously or intuitively, the criterion of wide-spread occurrence of a structure may provide valuable hints, especially if complexity provides an additional one. At this point the methodology touches on the problem of homology of a wide-spread structure which cannot be treated in detail here. With the help of the homology criteria, recently improved and refined by Hennig (e.g. [31,32]), one can identify similarities between species as homologous or not. If a similar structure of several species is not homologous, it can by definition be only an analogous character, that is to say a convergence which has arisen under the same selection pressure. At that stage one does not yet know which selection pressure has shaped the character under study, but one can be confident that it has (or had) the same function in the array of species under consideration. As is well known homologies need not have the same function.

Considering the criteria of complexity and constancy, one can confidently assume that many complex behaviour patterns or conspicuous structures the function of which is as yet not understood, *do* have to fulfill a definite service; for instance, anting in birds (i.e. the placement or rubbing of living ants in or at the plumage), the mobbing of a host of bird species upon predators, or the 'humps' of membracid bugs and many other characters, belong to this category.

The range of validity of the economy principle

At the beginning of each study of survival value Tinbergen[14,33] put the important question 'Has this trait of the organism any survival value?' This question would lose its sense if the economy principle were universally true. Assuming that it were true, there would be no organs or behaviour without function, except for the temporary state of rudimentation, i.e. after the selection has ceased which had previously shaped the adaptation.

Recently the economy principle has received forceful support by the new mathematical-physical treatment of the theory of selection by Eigen[6], which Schuster[7] published anew in a simplified version. Based upon facts of molecular biology and thermodynamic mathematics, Eigen shows that evolution has been an inevitable process once certain material conditions (nucleic acids, proteins) prevailed. Furthermore, according to the new theory, characters devoid of a function ('parasitic couplings') are shown to be eliminated. This latter postulate, which has been derived for probiontic systems, receives support from the investigations of Spiegelman[34] (vide [6,7]) on $Q\beta$-phages which, when food is superabundant and the bacterial host is not available, lose their ability for infection but instead reproduce much faster than before. For a decision of the validity of the economy principle, it remains a crucial question whether the reduction of formerly functional characters after the responsible selection ceases, can be extended to encompass all organisms. As soon as one leaves the level of deductive-mathematical reasoning, the question cannot be answered cogently unless one introduces, step by step, new parameters which do justice to the complexity of eubiotic systems. This has not been done so far (Eigen in lit. Dec. 1972). What remains in this domain of research is at present merely to formulate rules the inductive basis of which must neccessarily be highly diverse.

The wide-spread reduction ('regressive evolution') of eyes and of pigments in cave animals[35] and in endoparasites[36], or the reduction of innate enemy recognition by birds in enemy-free environments[37,38] (see also [39–42]), bear witness that characters the epigenesis of which almost certainly demands energy are maintained only through permanent selection. However, observations such as these cannot prove an all-encompassing validity of the economy principle, even if their number were unlimited. Likewise, knowledge of the numerous and allegedly functionless vestiges will not help to settle the question, for, firstly, one would have to assume that all of them were observed during their phase of becoming a vestige and it would be only a question of time until they totally disappear and, secondly, one would have to assume that such regressing characters had not taken over a new function or had maintained a partial function where selection has remained intact. Recently more and more cases have become known in which allegedly functionless structures prove to be highly functional (Osche in lit. Dec. 1972). For example, the widely known and accepted textbook story of the vestigial bones of the pelvic girdle of whales (*Delphinapterus leucas*) have the function of serving as insertion points for the penis muscles and for the insertion of muscles for closing the anus in both sexes[43].

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[30] A. J. Kalmijn, J. exp. Biol. *55*, 371 (1971).

[31] K. Günther, Fortschr. Zool. *14*, 269 (1962).

[32] W. Wickler, in *Die Evolution der Organismen*, 3rd. edn. (Ed. G. Heberer, Thieme, Stuttgart 1967), vol. 1.

[33] N. Tinbergen, in *Ideas in Modern Biology* (Ed. J. A. Moore; Proc. XVI. Int. Zool. Congr., Washington 1965).

[34] S. Spiegelman, in *The Neurosciences*, 2. Study Program (Ed. F. O. Schmitt; The Rockefeller University Press, New York 1970).

[35] A. Vandel, *Biospéleologie* (Gauthier-Villars, Paris 1964).

[36] G. Osche, *Die Welt der Parasiten* (Springer-Verlag, Berlin, Heidelberg, New York 1966).

[37] E. Curio, Proc. XIII. Int. Orn. Congr. (1963), p. 206.

[38] E. Curio, Z. Tierpsychol. *26*, 394 (1969).

[39] W. Pfeiffer, Z. vergl. Physiol. *52*, 79 (1966).

[40] J. D. McPhail, J. Fish. Res. Board Can. *26*, 3183 (1969).

[41] B. H. Seghers, Am. Zool. *10*, 489 (1970).

[42] H. M. Feder, Scient. Am. *227*, 93 (1972).

[43] A. V. Yablokov, Zool. Zh. *42*, 441 (1963).

Certain organs appear only in the embryo, as for instance the teeth of whales which no longer erupt or the vestigial Anlage of the egg tooth of marsupials which since hundred billions of years no longer incubate eggs[44] (see also [45]). Finally, latent potentials for behaviour patterns may remain completely hidden and can sometimes be identified as 'historical remnants' of former adaptations provided the phylogeny of the species under consideration is wellknown[32]. Thus some rails and doves which secondarily have become tree nesters roll in eggs which have been placed upon an artificial collar around their nest; the egg rolling movement cannot have been functional since these birds have become tree nesters and each egg which got out of the nest would be doomed to perish[46]. Likewise by manipulation of the eggs one can elicit filial following behaviour in the young of a cichlid fish (*Tilapia macrocephala*), a behaviour pattern which would normally remain 'dormant'[47].

Such hidden potentials have become part of the 'cryptotype' (OSCHE[13]), due to highly diverse processes, so that selection can no longer operate upon them[48]. The possibility that such hidden potentials become reactivated later on, and their wide-spread occurrence, bear witness of their fundamental role in the evolutionary process.

The maintenance of such potentials, as well as the allegedly functionless vestiges, can be theoretically interpreted in two ways. First they could be organizers for the induction of vital structures[48]. Second they might be controlled by pleiotropic genes which are indispensable for the epigenesis of vital structures[49]. So far, to the best of my knowledge, no proof of one or the other assumption has come to light. The majority of characters which are thought to be selectively neutral are 'end structures' (numerous examples in [49]) which hardly can induce the formation of other characters. This fact is evidence against the first hypothesis attesting an organizer function to such structures. On the other hand, the pleiotropy hypothesis remains theoretically unsatisfactory as well, since pleiotropic gene effects are but one mode of growth control which in itself could be the product of selection; if this is true, one cannot readily see why pleiotropy should not be reversed by suppressing certain effects of the underlying gene control if selection has become different. As demonstrated in the moth *Ephestia kühniella*, different effects of the same gene may be modified differently for dominance; and presumably some could be suppressed altogether if undesirable and if the gene were common enough as the wild type alleles normally will[50]. Irrespective of the impeccability of both objections, it will be profitable to keep in mind that both hypotheses explaining adaptively neutral structures rest upon our ignorance and upon lack of imagination. The experimental study of adaptations has unravelled adaptive values in such unobtrusive and inconspicuous details of organismic organization that one should think of a character as having survival value until the contrary has been demonstrated[14,33].

According to still another hypothesis, one could assume that the building-up of a hidden potential during ontogeny requires such minute amounts of energy that natural selection could not 'measure' them. Consequently the economy principle would have a zone of 'unsharpness' in which it would not be valid or only to a markedly low degree.

Hormones are a particularly apt means for eliciting hidden potentials. If testosterone is injected into female Canaries, they begin to sing, although they normally do not exhibit male song[51]; similarly female rats display male copulatory behaviour if treated in the same way[52] (see l.c. for further examples). Furthermore, the Platy (*Xiphophorus maculatus*) is the only species of its genus which has fragmented its epigamic display to such an extent that the fragments cannot be readily homologized with the display of other xiphophorine species. After application of testosterone the display fragments become integrated into a coherent display pattern similar to that of other congeners[53]. Particular significance in this context has to be attached to the following case. The formation and/or the pigmentation of the sword of the caudal fin of males of certain Xiphophorini can be induced in the males of species which normally do not possess a sword (Figure 2). This result is still complicated by the fact that in some species the dorsal finrays, too, form an incipient sword under the influence of the hormone, although none of the sword tail species possess a comparable structure[54,55]. The 'zone of unsharpness' would have to be regarded as comparatively small in such cases, while hidden potentials such as the ones described above could be due to neuronal patterns which had been built up before the eliciting agent was applied, that is to say that they had already required energy. By contrast the formation of an artificially induced sword would merely require a particular predisposition of the genome which then becomes activated by an unnaturally high dose of hormone. Thus, in the latter case, the economy principle would appear to be least invalidated. The

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[44] G. DE BEER, *Bildatlas der Evolution* (Bayr. Landwirtschaftsverlag, München 1966).

[45] A. E. EMERSON, Evolution *15*, 115 (1961).

[46] H. POULSEN, Vidensk. Meddr. Dansk naturh. Foren. *115*, 1 (1953).

[47] M. BRESTOWSKY, Z. Tierpsychol. *25*, 761 (1968).

[48] G. OSCHE, Zool. Anz. *174*, 411 (1965).

[49] T. DOBZHANSKY, Am. Nat. *90*, 337 (1956).

[50] E. CASPARI, Q. Rev. Biol. *24*, 185 (1949).

[51] H. H. SHOEMAKER, Proc. Soc. exp. Biol. Med. *41*, 299 (1939).

[52] F. BEACH, *Hormones and Behavior* (Hoeber Inc., New York 1948).

[53] D. FRANCK, Behaviour *30*, 76 (1968).

[54] M. DZWILLO, Verh. dt. Zool. Ges. Wien, *1962*, 152.

[55] C. D. ZANDER and M. DZWILLO, Z. wiss. Zool. *178*, 277 (1969).

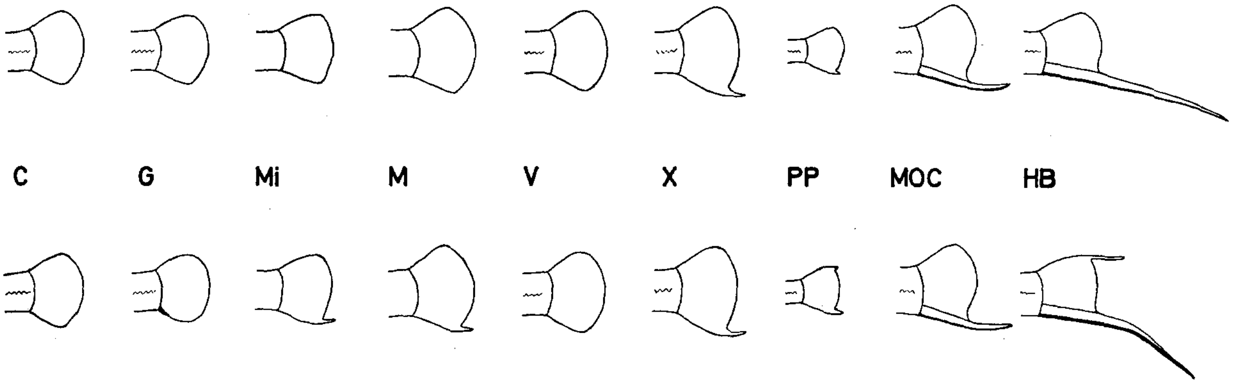

Fig. 2. Induction of a sword through application of methyltestosterone in the males of 9 *Xiphophorus* species; above: Normal form of the caudal fin; below: After hormone treatment (after ZANDER and DZWILLO[55]).

economy principle would even be strictly valid also in this case if the maintenance of unused genetic predispositions required no energy.

The interpretation of the manifestation of a sword by hormone application would be compatible with the concept of one of the modes of action of steroid hormones according to which they activate DNA to start morphogenesis[56]. However, the only proof for such action of steroid hormones so far has been the effect of ecdysone in chironomid midges[57,58]. The assumption of the maintenance of functionless genes would be in line with the theory by KIMURA and OHTA[59] (see also [60]) of the majority of all genes being selectively neutral. This theory, however, has already provoked heavy criticism from several sources[61,62].

Three major potential methods of teleonomy

The problem of selection of organs and behaviour patterns and their origin can be partitioned as follows:

1. Does a given character have adaptive value?
2. Which function (s) does a given character fulfill? This is equivalent to the question: Which selection pressure(s) has shaped it?
3. How great is the selective value of the character under study?

The first and most general of these questions makes sense only if one has good reason to assume that the economy principle is violated (see above), or if one can reasonably assume that the character under consideration is on its way to becoming a vestige, an assumption which would be compatible with the economy principle in its most rigorous form. In this latter case, however, one would have to know which function the very structure had to serve earlier (2nd question), because otherwise one could not decide whether the original selective force still existed or had ceased to operate.

It is fundamental to realize that conclusions about the function (biological significance) of a structure can only be drawn if organisms are compared which differ in an aspect of this structure from each other. This follows cogently from the selection principle which causally explains only relative differences of individual fitness but not absolute degrees of adaptedness. If one elaborates upon and extends a pioneer effort towards formalizing teleonomy by TINBERGEN[14], one can apply singly or in combination the three following major methods:

I. *The method of correlation* is an old one which has long been applied in functional anatomy (e.g. [63]). It seeks the selective agent(s) responsible for a character by correlating peculiarities of different species to their environment. Each environment harbors many selective forces. This fact, and the existence of compromise solutions which are due to the presence of highly diverse selective forces, cause difficulties in applying the method. Correlations are a) ecological sensu lato, i.e. they are 'Passungen' between organism and environment, b) intra-specific and c) intra-individual, then called co-adaptations.

a) *The ecological correlation*

In order to find out whether a given trait is an adaptation, or, if this has been affirmed, which selective force has given rise to it, a couple of rules utilizing probabilities can be applied which have already

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[56] C. D. TURNER and J. T. BAGNARA, *General Endocrinology* (Saunders, Philad. London, Toronto 1971).
[57] P. KARLSON, J. Cell comp. Physiol. *66*, 69 (1965).
[58] P. KARLSON and C. E. SEKERIS, Rec. Progr. Horm. Res. *22*, 473 (1966).
[59] M. KIMURA and T. OHTA, Nature, Lond. *229*, 467 (1971).
[60] M. KIMURA and O. TOMOKO, *Theoretical aspects of Population Genetics* (Princeton Univ. Press, Princeton 1971).
[61] M. G. BULMER, Nature, Lond. *234*, 410 (1971).
[62] L. BULLINI and M. COLUZZI, Nature, Lond. *239*, 160 (1972).
[63] F. BÖKER, *Einführung in die vergleichende biologische Anatomie der Wirbeltiere* (Fischer, Jena 1935, 1937), 2 vol.

proved to be useful strategies. On the one hand, one can facus attention upon a trait and examine whether it occurs in some environments more often than in others. A thorough comparison of all environments utilized will then show that one of several possible selective agents correlates best with the occurrence of the trait examined. This approach ('Reihenmethode'[64]) leads to

Rule 1. A given character may be regarded an ecological adaptation with increasing confidence the more of its possessors have evolved it in similar environments and the less those species are related with each other.

Thus locomotion in arthropods displays several independently acquired adaptations to different environments (crevices, cave walls, surfaces permitting unimpeded walk), and there are relations with certain modes of life (climbing, burrowing etc.); the convergent adaptations are coupled to a typical environment ('Lebensraumfaktoren – gekoppelte Analogien', historically but less aptly called 'lebensformtypische Analogien'). Rapid walk on obstacle-free surfaces is correlated in spiders, crustaceans, and insects with long but few legs (MANTON in [32]).

On the other hand, one could start with a supposed selection pressure and ask how precisely a presumed adaptation is coping with it. For this purpose, species of a closely knit group, optimally geographic representatives of one species, are studied in order to trace the 'raw material' which has given rise to the supposed adaptation. In the Galapagos Islands, birds of prey and owls exert selection pressure upon the terrestrial birds which is graded as a function of the number of predators and their density. DARWIN's Finches (*Geospiza* spec.) suffering maximal pressure from those predators have more inborn fear from them than those on predator-free islands. Similarly, the finches do not fear mammalian predators which are absent from the Galapagos biota but which are feared by song-birds of many regions where mammalian predators occur[38] (see also [65]). The Three-Spined Stickleback (*Gasterosteus aculeatus*) of the Chehalis river in Alaska has black-bellied males, the distribution of which coincides precisely with the occurrence of a potential predatory fish (*Novumbra hubbsi*) which is attracted by the normal red-bellied males to a much greater extent. In addition young Sticklebacks escape from the predator more successfully in the area of common occurrence than young from other areas[40] (see also [41]: *Lebistes reticulatus*). Further, rather precise adaptations have been evolved in mimicry systems where the discriminative power of a deceived signal receiver has been the selective agent (for example [66,67]).

The correspondence between a presumed or established selection pressure and the degree of adaptation are equivocal as long as one cannot exclude that factors varying in parallel with the presumed selective agent have not led to the observed character as well, particularly if the correlation discovered is rather loose. If such concomitant factors can be ruled out, the degree of correlation mirrors the degree of adaptation achieved. If an adaptation on these grounds appears comparatively imperfect, this may have many reasons, one fo which might be the strength of the responsible selection pressure. [It can be measured indirectly by the speed of the shift of gene frequencies per generation effected through selection (WRIGHT[68])]. Further rules can be utilized in the study of adaptations when there is only one species at hand:

Rule 2. Sudden changes during ontogeny are reckoned to be due to ecological adaptation with increasing confidence the less expectedly they appear epigenetically.

Rule 3. Adaptations identified in this way can be regarded as the effect of a particular environmental factor with increasing confidence the more closely they coincide with its action.

In Jamaica the brown larval variant of a neotropical hawkmoth (*Erinnyis ello*) rests during day-time on the trunk of its food plant or on the ground beside it, and thus escapes predators hunting in the foliage. An anole lizard (*Anolis lineatopus*) which hunts in the near-ground trunk region as the only predator is capable of foraging on larvae up to 5 cm of body length; larvae only 0.5 cm longer can scarcely be swallowed and longer ones not at all. The brown larvae acquire their colouration only after the last larval molt, i.e. after the IVth instar when they have reached a length of 4 cm and when they are still green. Only after growing to a body length of 5 cm, that is to say close to the upper prey size limit, do they daily wander down to their trunk resting place and will pupate when having reached a size of 9 cm. The start of resting on the trunk coincides rather remarkably with the relaxation of the enemy pressure but not, as might be expected, with the molt-related colour change[69]. Similarly, the ontogeny of the flight response of the Florida Apple Snail (*Pomacea paludosa*) fits exactly the upper prey size limit of one of its most formidable turtle predators (*Sternotherus minor*)[70]. An established correlation comes close to being a proof if the ontogeny of a given character does not change in only one direction but reverses by following the switch of the responsible selective agent or, still more convincing,

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[64] A. REMANE, *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik* (Geest & Portig K.-G., Leipzig 1956).

[65] E. CURIO, Experientia *17*, 188 (1961).

[66] P. M. SHEPPARD, Cold Spring. Harb. quant. Biol. *24*, 131 (1959).

[67] V. G. SPRINGER and W. F. SMITH-VANIZ, Smithson. Contr. Zool. *112* (1972).

[68] W. C. ALLEE, A. E. EMERSON, O. PARK, T. PARK and K. P. SCHMIDT, *Principles of Animal Ecology* (Saunders Co., Philadelphia, London 1967).

[69] E. CURIO, Z. Tierpsychol. *27*, 899 (1970).

[70] N. F. R. SNYDER and H. A. SNYDER, Behaviour *40*, 175 (1971).

if the development of a structure oscillates between its formation and its regression concomitantly with the supposed selective agent. The free-living Miracidium larvae of certain flukes have eyes which disappear in the parasitic instars, for instance in sporocysts living in an intermediate host while they reappear again in the free-living cercariae and finally disappear in the adult fluke living in the final host[36]. In order to evaluate the selection pressure which has led to the development of eyes, it is, of course, not necessary to search for such ontogenetic oscillations of developmental direction; however, the example illustrates how one could proceed in other cases involving a more enigmatic selection pressure.

Rule 4. Complex structures or performances may be regarded as being due to a particular environmental factor, the more of their component characters can be related point by point to this factor.

This rule of complexity is basically related to the economy principle (see p. 1047, 1048), but it claims to encompass more at this point of the argument. While the study of the enery needed for a particular structure only leeds to the conclusion that this structure is probably adaptive, the intricate point-by-point correspondence after rule 4 permits one to identify the selective force itself. Thus from many structural peculiarities of the eye of vertebrates or of cephalopods, in connection with the physics of electromagnetic radiation, one can arrive at the main function, namely vision[4]. This conclusion remains nonetheless true even if one finds many peculiarities of eye structure which can be understood functionally only once their connection with more central nervous structures has been unravelled. Basically in the same way one can trace the functional history of control systems ('Funktionsstrukturen') which are not accessable to direct observation. The perceptual correlates of the IRM of the Pied Flycatcher (*Ficedula hypoleuca*), serving to recognize shrikes as enemies[37], correlate with such precision with colour characters of shrikes that the conclusion is inevitable that only this group of songbirds has selected for this perceptual performance (CURIO, Anim. Behav., in press). A corroboration has been found in the geographical correlation between shrike recognition and shrike distribution[37,65]. In this connection the deprivation experiment, i.e. the experiment depriving an animal of a specific experience, plays a crucial part. After having established a close relation between signal receiver and signal emitter, as in the case of the Pied Flycatcher just mentioned, only the deprivation experiment can answer the question whether this stimulus response relation has been individually acquired or has been selected for by the pressure of the signal emitter. In case the experimental answer is positive, i.e. if recognition is innate (that is functions independently of the possibility of individual experience with the very stimulus situation the innate recognition of which is examined), then at least one of the selection pressures has been identified which have shaped the IRM under study. The precision of the stimulus response relation will then, in general, determine whether one has to look for further pressures.

The criterion of complexity (rule 4) can be readily applied much more broadly in the search for an unknown function not only of organs or behaviour patterns. The criterion can be profitably utilized also with variants of a species, and the result yielded is particularly clear if they vary discontinuously, that is to say in systems of polymorphism or phase variation[71]. For instance, the resting behaviour of larvae of the afore mentioned Hawkmoth is predictably coupled with larval colouration as a function of the hunting strategy of predators in two different Hawkmoth populations (Table I). While in both places the brown larva rests on the wooden parts of the food plant where it is highly cryptic, the green larva remains in the green foliage permanently, thus behaving again identically in the two populations. It is the blue larva which differs in its resting behaviour by remaining in the green foliage in Jamaica, like the green form and by wandering to rest at a brown branch on Galapagos, like the brown form where it is similarly concealed from view. In accordance with this population-specific behaviour of the caterpillars, the hunting strategy of the predators varies: In the Galapagos birds hunt by vision in the foliage for insects and such predators are, after all, deceived by cryptic coloration. By contrast, in Jamaica wasps (*Polistes crinitus*), which do not use colour vision for discovering their larva prey and thus cannot be deceived by concealing coloration, restrict their hunting behaviour to the foliage and ignore the trunk. Only the anole mentioned hunts in this latter region, and as has been experimentally demonstrated, it rejects *ceteris paribus* only the brown larva and attacks the green and the blue once an occasion arises (this is rather surprising since even an optimally cryptic prey loses its protection from visually hunting predators once it moves). The twofold enemy pressure namely that through the wasps 'from above' and the other through the anole 'from below' satisfactorily explains the deviant variation of the resting behaviour

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[71] Polymorphism is discontinuous intraspecific variation which is determined only through the genome; variants or morphs are common enough to rule out their presence as due to recurrent mutation[72,73]. The term has been applied, particularly in the entomological literature, to another mode of discontinuous intraspecific variation which, however, is epigenetically determined by environmental factors so that the individuals affected are genetically identical In this case one ought to say phase variation. or, still better, polyphenism[74].

[72] E. B. FORD, Biol. Rev. *20*, 73 (1945).

[73] E. B. FORD, *Ecological Genetics* (Chapman and Hall Ltd., London 1971).

[74] E. MAYR, *Animal Species and Evolution* (Harvard University Press, Cambridge, Mass. 1963).

in both populations. In both cases the caterpillars optimize their concealment and thus their enemy avoidance.

On the one hand, a polymorphic system can be interpreted in such an ecological way the better, the more morphs it contains. On the other hand, one has to consider that differences between the morphs neccessarily dwindle the more numerous the morphs become; then the point-by-point correspondence between each morph and its sub-niche will become increasingly difficult. Moreover, the 'grain' of the niche of a species neccessarily has an upper limit somewhere but it remains true that the complexity rule can be examined in polymorphic systems the more successfully the more heterogeneous their species-typical niche is. The complicated relation between the 'grain' of a niche and polymorphism has been treated so far only theoretically (e.g. [75]).

The rules propounded here for the search of adaptations and the underlying selective forces are by no means complete. They are thought to illustrate the way in which further rules could possibly be evaluated. The rules presented so far badly need a stronger formalization if teleonomy is to succeed and take its firm place in biology.

As long as particular ecological factors have to be viewed only as potential selection pressures, their identification will always need much imagination and intuition. The search for selective forces is considerably facilitated if one investigates problems of adaptation for which it is compulsory for the organism to attain a solution. This is the case with climatic conditions (e.g. [76, 77]) or relations between only two species as in many symbiotic or parasitic relationships. For instance, numerous orchids are bound to be cross-fertilized by only one hymenopteron, the males of which are deceived by the visual appearance and/or the particular scent of the flower which they take to be a female. When the male is to copulate with the orchid flower, the pollinia stick to its head and are transferred to the next flower of the same orchid species[78]. Relationships such as these are particularly amenable to experimentation because one need not search for the selecting agent, instead one needs merely to examine how selection operates.

Table I. Resting sites of the Vth instar larval forms of a neotropical hawkmoth (*Erinnyis ello*) in relation to the hunting strategy of their predators (after Curio[69]).

Diurnal resting site	Larval colour forms					
	Galapagos			Jamaica		
	green	blue	brown	green	blue	brown
Foliage	+			+	+	
Branch/trunk		+	+			+
Hunting strategy	Songbirds visually searching at all sites			Anole visually lurking at trunk. Wasps searching non-visually in foliage		

b) *The intra-specific correlation*

What just has been said about obligatory selective forces also holds true in this case: The conspecific organism is for the purpose of reproduction, at least in bisexual and dioecic organisms, indispensable. The problem then is to which characters of the conspecific an organism has to adapt itself. From the vast number of characters which might exert selection, one has to regard potential candidates in the search for a counter-adaptation, the fewer the better one knows the biology of a species. Thus, if one wants to know the adaptive value of the number of tits in female mammals one would not relate it to any character of the young to be nourished but to litter size. The example illustrates that if one correlates intraspecifically characters which presumably evolved when interacting with each other, one has to know beforehand an underlying selective force and its mode of operation; therefore this approach is less apt to identify a major selection pressure than to examine whether it was the only one which had shaped the character under study. The suspicion arises that there may be more than one selective force if the correspondence found is 'bad'. Basically the 'goodness' of fit can be judged after its compexity (rule 4). Because of their chance coincidence of many morphogeneses which are functionally unrelated, the potentially available criterion of the sudden change of the ontogeny of a given character (rules 2 and 3) appears to be inapplicable.

The strictly species-specific courtship songs of grasshoppers (*Chorthippus*) probably serve, to the exclusion of other functions, proper copulation as evidenced by the precision of recognition between the singer and the listener[79], or by the exact temperature compensation of singing and hearing in both partners[80]. Similarly, frequency sensitivity in the ear of the bullfrog (*Rana catesbeiana*) is tuned rather precisely to the energy spectrum of the mating call of the male which is also species-specific[81, 82]. By contrast, some songbirds analyze tone frequencies which exceed their own sound production, perhaps due to an additional

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[75] R. Levins and R. H. MacArthur, Am. Nat. *100*, 585 (1966).

[76] C. Kendeigh, Auk *66*, 113 (1949).

[77] C. Kendeigh, Ohio J. Sci. *66*, 369 (1966).

[78] L. Stebbins, *Variation and Evolution in plants* (Columbia University Press, New York, London 1963).

[79] A. C. Perdeck, Behaviour *12*, 2 (1958).

[80] D. v. Helversen, J. comp. Physiol. *81*, 381 (1972).

[81] R. R. Capranica, Am. Zool. *5*, 693 (1965).

[82] L. S. Frishkopf and M. M. Goldstein, J. acoust. Soc. Amer. *35*, 1219 (1963).

adaptation to the timely detection of stalking predators[83]. Such unsharpness of adaptation is not surprising when confronted with any 'multi-purpose' organ. Even within a species, song, for instance, may serve quite different functions[84]. Furthermore, the chicks of at least five species of Gulls respond with suboptimal begging to the colour signals of their parents' head[85] (and CULLEN verbal communication), and the attachment of the young of several cichlid fish does not correspond very well or only coarsely to the colour pattern of the guiding parent (e.g. [86]). Such incongruences between signal emitter and signal receiver indicate that more than one selection pressure and possibly one from each side of the system has been at work.

c) *The intra-individual correlation or co-adaptation*

At each moment of its evolution, a species needs to be adapted to its environment and so must be every single character. Since these form a harmonically organized whole, they need to be co-adapted to each other. The underlying genetic homeostasis extends to the capacity to respond homeostatically also to environmental forces which tend to shift the physiological balance within the organism. Because of this intricate relationship between the parts, the development of a new adaptation causes others to follow in its wake. Since all this occurs in small steps, it is often difficult to decide which of several selection pressures was a primary one, causing others to follow. On the other hand, the evolution of an adaptation can lead as well to a relaxation of pressure in other contexts and thus may lead to regressive evolution, the outcome of which may then not neccessarily be different from the effect of relaxation of an environmental selective agent. In this way rudimentation of a character may draw attention to traits, the adaptive value of which has been previously overlooked[87].

Examples illustrating the nature of coadaptations are animals with effective defensive weapons or with defensive excretions, most species of which are more fearless than less well-protected species (e.g. [88,89], further ethological examples in WICKLER[90]), or species with a high mortality of early developmental stages have a high compensatory reproductive rate, etc. Starting from the principle of such compensations, MACARTHUR[91] formulated two opposed principles of natural selection, i.e. r- and K-selection which are but the extreme ends of a whole spectrum of modes of selection in between. The justification of this dichotomy has recently been substantiated experimentally in populations of Dandelion[92]. According to this dichotomy, species with predominantly density-independent mortality experience a selection which results in a high reproductive rate, at the expense of mechanisms which protect the species against enemies and competitors. On the other hand, species with mainly density-dependent mortality are K-strategists, i.e. they have a reversed distribution of their available resources. It remains to be seen in how far the concept of these two opposed adaptive strategies will serve as a guide for search on the selection pressures; the syndrome nature of so many adaptations, as they pervade the biology of a species (examples [90,93]), makes this appear probable.

II. *The method of altering a character*

This approach serves to attain two goals: The physiologist applies it in order to unravel the functioning of a given physiological performance by altering part of the machinery; he then examines how this affects the efficiency of the functioning of the mechanism investigated. The evolutionist also alters an organ or a piece of behaviour and then looks to what extent the altered organism survives and thus reproduces, as compared to organisms which have remained unchanged. If such experiments are well designed they provide an answer to the questions of the responsible selective agents, their mode of operation and the problem of the selective value of the manipulated character[33].

Because it is notoriously difficult and even impossible to alter a character without altering others, one has to rely most often on a 'natural experiment'. In essence one compares the survival of animals which, for instance, display in a given situation a behaviour coping with the situation, with that of conspecifics which under identical circumstances fail to show the behaviour in question. For the evaluation of the ensuing observation it is, in a first step of the analysis, entirely irrelevant whether the behaviour under study is restricted to particular variants of a species or whether it occasionally occurs in one and the same individual. In the realm of morphology, only the former

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[83] M. KONISHI, Z. Vergl. Physiol. *66*, 257 (1970).

[84] G. THIELCKE, Vogelwarte *25*, 204 (1970).

[85] D. A. QUINE and J. M. CULLEN, Ibis *106*, 145 (1964).

[86] P. KUENZER, Z. Tierpsychol. *25*, 257 (1968).

[87] Co-adaptations, the components of which have no selective value at all in the absence of the complementary components, i.e. the 'synorganizations' of REMANE[64], do not lend themselves to such an evaluation. If neccessitated, such co-adaptations can only form or regress as a functional whole with the constituent components only being altered simultaneously. An example is the coupling device which interconnects the hind and the forewing of many flying insects.

[88] R. HOOGLAND, D. MORRIS and N. TINBERGEN, Behaviour *10*, 205 (1957).

[89] K. J. WILZ, Z. Tierpsychol. *29*, 1 (1971).

[90] W. WICKLER, *Verhalten und Umwelt* (Hoffmann und Campe, Hamburg 1972).

[91] R. MACARTHUR, natn. Acad. Sci. Proc. USA *48*, 1893 (1962).

[92] M. GADGIL and O. T. SOLBRIG, Am. Nat. *106*, 14 (1972).

[93] M. CULLEN, Ibis *99*, 275 (1957).

method (see below III.) is applicable for a structure of a given individual can only be present or be absent. Various snake species (Colubridae, Leptotyphlopidae) occasionally display one or a number of protective behaviour patterns directed against their enemies which are snake-feeding snakes (*Lampropeltis getulus, L. triangulum*). Encounters under controlled conditions between prey and predator revealed that defensive behaviour led to survival more often than inactivity[94]. Similarly, CRANE[95] (fide [96]) found that preying mantids were seized and eaten by monkeys and insectivorous lizards when offered to these predators only if they remained static instead of displaying aposematic colour patterns. In experiments such as these, one has carefully to observe that the individuals to be compared with each other do only differ in the very character the function of which one is going to examine. This fundamental premise was violated by ROEDER and TREAT[97] when they related the successful escape flight of nocturnal moths from hunting bats to the presence of the capacity of hearing alone and thereafter computed a relative selective advantage of 40% to that capacity, a data which has entered the secondary literature several times. Such result would be conclusive only if it were to have been derived from a comparison of hearing and non-hearing representatives of one and the same species. For it remains unknown by which other characters than hearing the moths might have additionally increased their chance of survival. Furthermore, another caution demands that only such individuals must be compared with each other which have not ceased to reproduce since natural selection is measured by differential reproductive success (see above). Otherwise one would have to prove, or would have to assume, that the character under study would not change after reproduction has ceased, and/or that the character would be of selective value also after that point. The latter possibility, however, applies to relatively few species which live in social groups, the members of which are more closely related with each other than with other family groups, and in species in which sterile animals contribute their share to the survival of younger group members.

The question of the adaptive value of some character can be tackled systematically only by altering or eliminating it. Thus HOOGLAND, MORRIS and TINBERGEN[88] cut off the spines of three- and tenspined sticklebacks (*Gasterosteus aculeatus, Pygosteus pungitius*) and then offered the despined fish to relevant predators as pike and perch. This procedure resulted in the despined fish falling more often prey to their predator than those left in the natural state. The predator learned to avoid threespined sticklebacks, less so the tenspined ones, after very few encounters with them; even normal threespined sticklebacks already seized were sometimes spit out still unhurt after the spines had inflicted pain in their predators snout. From this evidence it can be concluded that the spines provided a relatively high degree of protection from predators, albeit not an absolute one; at the same time part of the responsible selective agents had been identified for the experimental predatory fish are a real threat in the wild.

Given two premises, such selection experiments could provide the basis for the calculation of the relative selective value of the character under investigation (see below III.): 1. The experiments must be conducted under natural conditions i.e. if possible in the wild where evolution took place. 2. If the character under study fullfills more functions than the one examined, the computation of the entire selective value has to take into account the single selective values of all functions identified. Both these conditions are not fulfilled in the experiments described so far since these took place under artificial conditions and because the spines of the threespined stickleback serve yet another function. If the territorial male courts a female ready to spawn, he chases her away at intervals in order to self-regulate his sexual tendency by pricking her with erect dorsal spines so that she flees before returning shortly after; his activities almost imperceptibly grade into sexual behaviour so that spawning is finally achieved[98]. Thus the dorsal spines serve at least two entirely different functions, the selective value of which has to be measured in each case.

In basically the same way as has been followed up with the sticklebacks' spines, one can investigate the adaptive nature of inter-specific relationships by removing one of the species involved. Thus ROSS[99], for instance, demonstrated that hermit crabs (*Dardanus arrosor, D. callidus*) which often carry on top of their shell an anemone (*Calliactis parasitica*) derive protection from it against an octopus (*Octopus vulgaris*).

The investigation of the adaptive value of a behaviour pattern meets, as a rule, more difficulty than that of a structure; because of the ubiquitous intricate interconnection of nervous control systems, a behaviour pattern cannot be readily altered or eliminated. In order to investigate the function of egg shell removal by blackheaded gulls (*Larus ridibundus*) after hatching of the chick, TINBERGEN et al.[100], for the first time and with great success, found a way out of this difficulty in that they changed the *effect* of a given behaviour pattern onto the environment and thereafter examined how the very change had affected the survival of the

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[94] F. R. GEHLBACH, Herpetologica *26*, 24 (1970).

[95] J. CRANE, Zoologica, N.Y. *37*, 259 (1952).

[96] M. EDMUNDS, Zool. J. Linn. Soc. *51*, 1 (1972).

[97] K. D. ROEDER and A. E. TREAT, Am. Scient. *49*, 135 (1961).

[98] K. J. WILZ, Nature, *226*, 465 (1970).

[99] D. M. ROSS, Nature *230*, 401 (1971).

[100] N. TINBERGEN, G. J. BROEKHUYSEN, F. FEEKES, J. C. W. HOUGHTON, H. KRUUK, E. SZULC, Behaviour *19*, 74 (1962).

individuals involved. Starting from simple observations, these workers examined if the presence of egg shells in the nest would disclose eggs and young chicks to predators such as herring gulls and crows; by doing this they began to put to the test one of five hypotheses on the function of egg shell removal in birds which had been put forward so far. Since blackheaded gulls of a colony communally attack predators with some success, eggs were laid out beside the breeding colony and concealed in a natural way. Subsequently one egg shell was placed beside each egg of an experimental group while the eggs of a control group were left unchanged. The establishment of an artificial colony beside the genuine colony aimed at eliminating the protection provided by the adults. A comparison between both groups of eggs revealed that an egg shell attracts the attention of avian predators to the artificial nests to an enormous extent (Table II). This proves that the carrying away of the egg shell by the parent birds provides protection for the brood from predators. The experiment, however, does not allow one to rule out the possibility that the carrying away of the egg shell might have further consequences for the brood. What was examined was merely the presence or the absence of an egg-shell at the nest but not the carrying away itself. This might have consequences as yet unexplored; a gull carrying away a shell, for instance, exposes its brood to danger if its brood mate is absent at the same time. Or other colony members could draw information on events in the nest of a parent gull which carries away a shell and this might have consequences for the brood, especially since many colonies suffer from blackheaded gull cannibals which are prone to prey on freshly hatched young not their own[100]. For these reasons, the protective value of egg shell removal might differ quantitatively from that which could be computed from the experiments mentioned if the behaviour pattern itself were investigated and not its outcome in relation to the shell, though at the moment this appears the only possible way of tackling the problem. Yet there is another reason why the adaptive value just established cannot be used for obtaining the relative selective coefficient of egg shell removal. This behaviour is but a part of a whole bunch of factors which tend to keep off enemies from the colony. Nests are dispersed widely and the eggs are cryptically coloured so that enemies have difficulty from both reasons in locating them[14,33]; the adult birds attack the predator etc. All these protective decives could normally interact with each other; their single selective values need not interact in a simple algebraic fashion. The relative selective value of each of these protective devices could consequently only be evaluated in the integral natural situation. To do this one would need blackheaded gulls which carry away their egg shells and others which fail to do it, and these two types of gull would necessarily have to be identical in every other respect; only then would a further method of teleonomy (which will be discussed immediately), be applicable. Since the blackheaded gull regrettably lacks the desired behaviour dichotomy in a reliable way, one has to look for more suitable subjects.

Table II. Proportion of blackheaded gull eggs robbed by predators as a function of an egg shell in a distance of 5 cm (modified after TINBERGEN et al.[100])

Egg with shell	Egg without shell
65% from 60	22% from 60
$P < 0.001$	

Experiments such as these, in essence, only permit one to conclude which selective force is maintaining at present some character under consideration; it does not reveal which forces have shaped it in the past. Only exceptionally is the adaptation investigated precise up to most minute details, so that selection factors other than the one envisaged can be ruled out with same confidence as a causative agent. Only then both effects can be ascribed to it (p. 1052). A neccessary prerequisite for proceeding in this way is that the selection pressure has remained stable in all those features which have shaped the adaptation observed.

III. *The method of variants*

This approach utilizes the natural individual variability of species by investigating the Darwinian fitness of different variants. Results obtained are particularly clearcut if one is able to study discontinuous variation of species, i.e. polymorphisms or polyphenisms or mixtures of both. The selection experiment has to take into account how far 'cryptic' characters of the organism, especially of its material composition ('cryptic' polymorphisms of FORD[73]), affect its outcome (solely).

In his classical experiments on selection operating on two colour types of the peppered moth (*Biston betularia*), KETTLEWELL[101,102] has, for the first time, succeeded in studying natural selection in the wild. He showed how insectivorous birds selected for the cryptic coloration of the moth during its diurnal resting. The *carbonaria* form which comprises the dominant homozygotes and the heterozygotes is nearly wholely black, while typical *betularia* is mottled black and white. *Carbonaria* enjoys a selective advantage as compared to *betularia* in industrial areas where the trunks of trees are dark from pollution, which moreover

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[101] H. B. D. KETTLEWELL, Heredity *9*, 323 (1955).

[102] H. B. D. KETTLEWELL, Heredity *10*, 287 (1956).

has eradicated the light coloured lichens so that the dark coloration matches better with the background. By contrast, in the natural habitat where lichens abound which make the trunks appear light, typical *betularia* enjoys a selective advantage as opposed to *carbonaria*. The mortality of both morphs was determined in two ways which do not guarantee each time that the moths could have selected their day-time resting place without interference from the experimenter. The moths normally select a background coloration just before dawn. As KETTLEWELL[103] demonstrated in captive moths which were offered a mixture of black and white backgrounds, the light coloured morph selects a light background while the dark morph selects a black one. (The evidence is statistically not particularly good but SARGENT[104,105] could meanwhile show both intraspecifically with polymorphisms as well as interspecifically that North American moths select a background matching their coloration). It remains questionable whether cryptically coloured moths select, after being disturbed through the release procedure, the proper background in the same way as when left undisturbed. In this regard it is important to note that the polluted industrial habitat and the natural habitat offer both light and dark coloured spots in the environment. If cryptic coloration and concealing behaviour are coupled with each other as just mentioned, both morphs might have selected when released those backgrounds which would have matched their coloration most profitably. In other words: the mortality of both morphs might differ more from each other under experimental than under natural conditions. Because of this, the morph-specific mortalities cannot serve as a basis for evaluating correctly the relative selective values of the deviant coloration per se.

It was not until the remarkable colour form-specific resting behaviour in the larvae of the aforementioned hawkmoth was discovered that a study of animals performing their undisturbed activities in the wild yielded an assessment of relative selective values of single characters. As revealed by selection experiments in Jamaica, the green, green-grey and blue last instar larvae which stay in the foliage of their food plant, suffer from a depredation which is eight times higher than that of the brown larvae which for many day-time h go down to rest on the trunk (see p. 1052). At their trunk site the brown larvae are practically safe from wasps which prodigiously and indiscriminately prey upon the non-brown larvae in the foliage. From the respective mortality data of both groups of larvae, a life expectancy for the foliage larvae of $E_f = 17.5$ day-time h can be computed which for the trunk larvae amounts to $E_t = 143.1$ day-time h. From this data the relative selective coefficient of the resting behaviour in the foliage then derives as $S_f = E_f/E_t = 0.12$, or, put another way, the trunk resters enjoy a relative selective advantage of ca $S_t = 0.88$, since $S_f + S_t = 1$[106]. Although this value of 0.88 has been corroborated by two more methods of assessment[107] one has to keep in mind that it has been assumed that the reproduction of the imagoes is not affected by larval variation.

As has been mentioned above (p. 1051, 1052), the brown *ello*-larvae enjoy an advantage derived from their colour pattern which protects them in some unexplored way from an anole hunting in the trunk region. The relative selective advantage of the brown larva due to its coloration has been assessed as $S_b = 0.92$ which adds to the aforementioned $S_t = 0.88$[69]. It is postulated that as yet unknown selective advantages of the non-brown larvae must compensate for their double disadvantage resulting from their deviant coloration and their deviant resting behaviour in order to account for their flourishing existence in the populations studied so far; it can already be stated with confidence that such compensatory advantages are related to factors other than predation in the larval stage.

Particularly suitable cases have offered the oportunity to assess Darwinian fitness of different morphs by estimating their reproductive success irrespective of how it comes about[108]. A complete understanding of such fitness differences will be gained only when it has been explored by which functional differences they are caused and which selective forces keep the morphs in balance with each other.

Appendix

Below are listed a number of surprisingly long-lived errors and misunderstandings about basic concepts of evolution which still nowadays hamper fruitful discussion and research. It is attempted to clarify issues which are thought to have been settled.

1. 'The totality of characters of a species is of selective advantage because the species survives'. However, selectively negative traits are commonly taken into the bargain by a species because they are balanced by selectively advantageous characters of the common underlying genes. This is typical of numerous polymorphisms, although the precise manner by which these are kept in balance may be vastly different[109]. In how far characters of an organism may be selectively neutral is still controversial (p. 1048). The error under discussion is related to the equation of optimal adaptation and survival. The equation overlooks that the outcome of selection is always determined by a

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[103] H. B. D. KETTLEWELL, Nature *175*, 943 (1955).
[104] T. D. SARGENT, Science *154*, 1674 (1966).
[105] T. D. SARGENT, J. N.Y. ent. Soc. *77*, 75 (1969).
[106] E. CURIO, Verh. dt. zool. Ges., 64. Tagung, 348 (1970).
[107] E. CURIO, Nature, Lond. *228*, 382 (1970).
[108] P. O'DONALD, Nature, Lond. *238*, 403 (1972).
[109] J. MAYNARD SMITH, Symp. zool. Soc. London *26*, 371 (1970).

differential reproductive success of diverse genotypes in a given environment. The flaw would in addition imply that individuals would be 'livelier' than others, which is clearly absurd. For the same reason no organism could be perfectly adapted to its environment, because this would imply that it would be immortal[110]

2. 'A particular character of species A can have no adaptive value because another species B in the same habitat lacks this character', a common flaw which Huxley[111] aptly epitomized as the 'refrigerator mistake' (a refrigerator is of no use because our grand parents survived without it). Again, it overlooks that selection only means intraspecifically different reproduction of genotypes which clearly cannot be compared in some species picked out deliberately. At the utmost, reproductive success can be compared in filial species that have arisen from a common ancestor or of a species and its subsequent progenitor. At the same time the error overlooks the inherent opportunistic nature of the evolution of adaptations which lead to their well-known bizarreness: The success by which a species solves a problem of adaptation does not depend upon the particular way of the solution[2].

3. 'The experimental evaluation of a function satisfies the need to look for further functions of the same character'. This 'error of exclussiveness' readily hides from the observer that more than one selection pressure maintains a particular adaptation. If it is at present really only one, formerly several others which have dissipated now may have operated in a similar direction (p. 1046). The exceedingly common compromise nature of adaptations indicates that, more often than not, several selection pressures which act in different directions, maintain them[12–14]. At the same time this explanation may harbour the interpretation of a sub-optimal adaptation to one selective agent.

4. 'Hyper-adaptations' denotes adaptations which are thought to achieve more than the environment demands[112]. Any evidence adduced in favour of the hypothesis of 'hyper-adaptation' would clearly violate the principle of natural selection. The underlying reasoning leaves out of account that adaptations have to cope with the worst conditions for survival equally well as with average or optimum conditions of life to which an organism is exposed; only insufficient sample size can lead to the conclusion that an organism performs beyond neccessity. Adaptations have a 'margin of safety' which helps to cope with the whole spectrum of values which can be taken by the environmental factors[17].

5. 'The survival of individuals after experimental elimination of a structure or behaviour pattern prove that they can be of no adaptive value'. Evidence such as this can only show that the character under study is dispensable. As can be demonstrated through a close comparison with the untreated control individuals, the elimination jeopardizes the vitality of the altered individuals and thus their chance of reproduction (p. 1055).

Further errors and misunderstandings have become increasingly infrequent in the scientific discussion so that it was felt unneccessary to point them out.

Zusammenfassung

Das einzige für die Biologie kennzeichnende Problem der Anpassung von Organismen an ihre Umwelt hat nicht die Bearbeitung erfahren, die es verdient hätte. Als einer der Hauptgründe für diese Lage wird das Fehlen einer formalisierten Methodenlehre für die naturwissenschaftliche Erforschung von Anpassungen, die Teleonomie, angesehen. Nach kurzer Streifung begrifflicher und ihrer Erforschung nach noch offenen Grundfragen, z.B. dem Ökonomieprinzip, wird ein methodischer Ansatz vorgelegt, mit dem Anpassungen entdeckt und ihrer Entstehung nach erforscht werden können. Die teleonomen Methoden umfassen 1. Das Aufsuchen von Korrelationen zwischen untersuchter Eigenschaft und Umwelt, die wie üblich weit oder aber eng, innerhalb der Grenzen des Organismus, gefasst sein kann. Die notorische Vieldeutigkeit solcher Korrelationen macht einer Deutung als Ursache-Wirkungs-Beziehung zwischen der Selektion und der von ihr geformten Eigenschaft dort Platz, wo sichergestellt werden kann, dass nur ein Selektionsdruck am Werke ist. 2. Die Veränderung einer Eigenschaft und die daran anschliessende Prüfung auf verschiedenen Fortpflanzungserfolg bei so veränderten und unverändert gebliebenen Gliedern einer Art. Verhaltensweisen, die sich im Experiment oft als unveränderbar erweisen, können auf ihre Funktion hin untersucht werden, indem man ihre Wirkung auf die Umwelt verändert und entsprechend den Fortpflanzungserfolg der betroffenen Individuen miteinander vergleicht. 3. Mit Hilfe von Varianten einer Art unter gleichen Selektionsbedingungen kann der Selektionswert einer Eigenschaft quantitativ ermittelt werden.

In einem Anhang wird versucht, einige der häufigsten Irrtümer und Missverständnisse klarzustellen, die auch heute noch einer erfolgreichen Teleonomie entgegenstehen.

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[111] J. Huxley, *Evolution, the Modern Synthesis* 4th edn. (Allen & Unwin, London 1945).

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