Summary

Intraspecific selection and the interrelationships between natural and sexual selection

Social behaviour patterns of animals all result from intraspecific selection. The exchange of signals between conspecifics is based on an extremely fine coordination of the actions of sender and receiver. In a reproductive context this coordination must be especially exact, as errors in partner choice lead to hybridization and thus to a waste of gametes. Nevertheless, hybridization does occasionally occur precisely in some bird families with highly evolved courtship behaviour; this however is not due to a malfunction of the signalling system, but to a particular behavioural faultconstellation in both sexes.

Although the development of courtship displays has originally been subject to selection pressures excerted by the opposite sex, the final form of a particular display has always been decisively determined by the environment. Counterselection through environmental factors occurs whenever the further development of a courtship display would mean too great a risk to the survival of the individual.

Literatur

Abrahams, C. N. (1939): A supposed hybrid whydah. Avicult. Mag. 43: 203—204. ● Darwin, Ch. (1871): The descent of man, and selection in relation to sex. London. ● Lill, A. (1976): Lek behavior in the golden-headed manakin, *Pipra erythrocephala*, in Trinidad (West Indies). Z. Tierpsychol, Suppl. 18. ● Mayr, E. (1972): Sexual selection and natural selection. In: B. Campbell, Editor, Sexual selection and the descent of man 1871—1971, 87—104. Chicago. ● Nicolai, J. (1975): *Geopelia cuneata* — Kopulation Encyclop. Cinematogr. E 1711. Göttingen. ● Ders. (1976): Evolutive Neuerungen in der Balz von Haustaubenrassen *(Columba livia* var. domestica) als Ergebnis menschlicher Zuchtwahl. Z. Tierpsychol. 40: 225—243. ● Roberts, A. (1926): Some changes in nomenclature, new records of migrants and new forms of S. African Birds. Ann. Transvaal Mus. XI: 217—225. ● Sielmann, H. (1967): *Paradisaea raggiana* (Paradisaeidae) — Balz und Kopulation. Encyclop. Cinematogr. E 1061. Göttingen. — Ders. (1967): *Ptilonorhynchus violaceus* (Ptilonorhynchidae) — Balz und Kopulation. Encyclop. Cinematogr. E 1077. Göttingen. ● Stresemann, E. (1930): Welche Paradiesvogelarten der Literatur sind hybriden Ursprungs? Nov. zool. 36: 6—15. ● Yamashina, Y. (1930): On a new subspecies of *Prosteganura haagneri*. Tori 6: 113—115. — Yealland, J. J. (1959): The national exhibition of cage birds. Avicult. Mag. 43: 203—204.

Anschrift des Verfassers: Priv.-Doz. Dr. J. Nicolai, Institut für Vogelforschung „Vogelwarte Helgoland", D-2940 Wilhelmshaven-Rüstersiel.

Die Vogelwarte 29, 1977, Sonderheft: 127—135

Toward an ecological morphology

By Walter J. Bock

Department of Biological Sciences, Columbia University, New York and Department of Ornithology, American Museum of Natural History

Introduction

Morphological tradition — that body of concepts, thoughts and techniques central to the historical development of morphology — has been one of a laboratory science ever since its beginnings in Greek antiquity and its later revival in the late Renaissance (Russell 1916). This tradition remained little changed through the Darwinian revolution and the replacement of earlier ideas of typology and essentialism with concepts of organic evolution. To be sure, mention was made frequently in morphological studies of the environment of organisms and of the interaction between structural features and ecological demands on the animal. Birds fly in the air and some, such as auks and penguins, fly underwater. The bill of finches is used to open seeds. Yet such statements are part of laboratory conceived investigations of the function of these structures rather than true ecological analyses. This laboratory tradition has permitted morphologists to make great advances in the explanation of biological form (e. g., Dullemeijer 1974, Gould 1973), but it is not sufficient for inquiry into all questions of central interest to morphologists among which are: How can the adaptive significance of structural features be ascertained?; How should morphological characters be studied comparatively with respect to analyses of phylogeny and of classification?; What are the evolutionary mechanisms by which new features and groups originate and diversify?; And, how should the evolutionary history of particular features and groups and groups be elucidated?

The laboratory tradition of morphology is essential, but not sufficient, to inquire into these questions about the adaptiveness and evolution of structural features. A complete and sufficient foundation for these inquiries can be obtained only if field studies, such as behavior and ecology, and if a historical perspective are added to the analyses of descriptive and functional morphology. Under the heading of ecological morphology and within the broader concept of evolutionary morphology (Bock 1969: 411—413, Bock 1974:124), I would like to examine the ways in which morphological tradition must be broadened to include those field studies essential to a sufficient foundation for all causal explanation of morphological features (= biological form). Because many of the methods and goals of this new area are still hard to visualize and articulate, I use the title „Toward an ecological morphology." Yet it makes little sense to present and support the belief that ecological morphology is an essential part of a broader morphological tradition without providing some practical suggestions on how these studies can be undertaken; some will be presented.

Although the idea that field studies — behavior and ecology — are essential in morphological research has never had an important role in morphological tradition (Davis 1949), it is not new. A slender thread of such thoughts has always existed in morphological history; a few examples will suffice. In 1875, Anton Dohrn, who founded the marine biology station at Naples in 1874, proposed the „Prinzip des Funktionswechsels" as a mechanism of evolutionary change. This concept was the first important general evolutionary principle dealing with morphology and macroevolution after the publication of „On the origin of the species." It is clear from his work that Dohrn regarded observations of living animals in their natural environment as an important part of morphological work. Sixty years later, Hans Böker elaborated on the idea of „comparative biological anatomy" which stands as the main part of the title of his two volume work „Einführung in die vergleichende biologische Anatomie der Wirbeltiere" published in 1935—37. Böker argued that functional observations, and even more importantly field observations of animals were essential if one hoped to understand the adaptiveness and the evolution of morphological features. Lastly, the two textbooks by J. Z. Young „The life of vertebrates" (1950) and „The life of mammals" (1957) illustrate the belief that the whole life history — the behavior and ecology — of animals should be part of a morphological text.

I would like to examine the development of ecological and of evolutionary morphology in terms of the ideas discussed by Ernst Mayr (1961, 1972) in his analysis of explanation in biology. Mayr distinguished between functional and evolutionary biologists, and showed how each group examined biology from very different perspectives. He expressed these different explanations by the concepts of proximal cause and of ultimate cause, and argued that a full biological explanation required both. Mayr stressed that progress in biology would not be possible so long as the functional biologists do not inquire into the ecological and the historical (= evolutionary) aspects of biological features, and so long as the ecological and evolutionary biologists regard the organisms under study as „black boxes" and do not inquire into the features and mechanisms operating within these black boxes. Clearly full explanation of any biological phenomenon requires contributions from both approaches.

Analysis of biological adaptation — the actual determination of individual adaptations and the formulation of general principles — cannot be achieved unless the work and ideas of both groups of biologists are joined. Investigation of the adaptiveness of morphological systems is especially well suited for delving into the matters posed by Mayr. The skeletomuscular system has special advantages because it is possible to inquire into the mechanisms of the „black box" of the skeletomuscular system at many levels of organization from the whole organism down to the level of fine structure and even to the macromolecular level. And it is possible to observe animals living freely in their normal environment using parts of their skeletomuscular system for feeding, locomotion, defense and what not.

Adaptation

An adaptation is a feature of an organism. It is almost of no interest to inquire into whether a whole organism is adapted to its environment — it must be, otherwise it would be dead. Rather, biologists are interested in the adaptive significance of individual features and how each adapted feature contributes to the survival or to the fitness of the organism.

Thus an adaptation is a feature which interacts with some factor of the environment of the organism such that the individual survives and reproduces. Stress is placed on the organism surviving as an individual because it cannot otherwise reproduce. But adaptations cannot be judged only with respect to survival as an individual; the organism must survive and reproduce.

Adaptations must be judged with respect to a particular environment and always on a probability basis with respect to present (and possibly past) environmental conditions, but never against future factors. The environment is the external environment, be it biotic or physical. Hence adaptation is defined and individual adaptations are judged with respect to selection forces arising from the external environment and acting on the organism. Adaptation does not designate relationships between parts of the organism or a relationship of a feature to the „internal environment." Notions such as „the internal environment" or „internal selection" are misleading to the extreme and should be abandoned. Muscles are not adapted to bones, but these anatomical systems are integrated ones that are adapted to selection forces arising from the external environment.

Each adaptation must be determined individually by direct analysis; the comparative approach is invalid for determining adaptations (Bock, ms.). Comparisons can be made only after the individual adaptations had been established. Recognition of adaptations depends upon careful separation and delimitation of properties of features and of the relationships between the environment and the organism. I will rely upon the set of ideas advocated earlier by von Wahlert and myself under the heading of „Adaptation and the form-function complex" (Bock & von Wahlert 1965). The relationship between these concepts are illustrated in Figure 1.

Adaptation, both the state of being and the process, must always be stated with respect to a particular environmental factor of the umwelt. Moreover, the feature is not adapted to the environmental factor but to the selection force resulting from the feedback interaction between the organism and umwelt factor. Hence adaptation must be defined and must be judged with respect to definitely delimited selection forces.

An adaptation is a feature of an organism that has at least one biological role interacting with a selection force — it forms a synerg. An adaptation, the state of being, can be defined as a feature having properties of form and function which permits the organism to maintain successfully the synerg between a biological role of that feature and a previously stated selection force. Note that the selection force must be given prior to the statement of the adaptation. By successful, I mean that the individual organism survives as an individual and reproduces to leave progeny in the next generation. Success is a relative term and some measure of success or of the relative degree of goodness of the adaptation is needed. Bock and & von Wahlert (1965: 286—287) suggested that the degree of adaptation could be judged by a measure of the amount of energy required by the organism to maintain the synerg — a sort of efficiency judgement. Hence the degree of adaptation, the state of being, is defined as the amount of energy required by the organism to maintain successfully the synerg of the stated adaptation with a lower energy requirement indicating a better degree of adaptation. Thus the degree of adaptation is inversely related to the energy required to maintain the synerg. It must be noted that the degree of adaptation is judged for a stated adaptation and that the adaptation is determined relative to a stated selection force. Energy requirements must always be given in terms of calories — gm-wt^{-1} to compensate for different body sizes especially in comparative studies. The adaptiveness of different individuals, either of the same or of different species, can be compared, but must be compared against the same selection force. This definition of the degree of adaptation is most useful for comparisons between closely related species and decreases in its usefulness as the degree of evolutionary relationship increases.

Energy utilization can also be used to indicate adaptive change as a feature requiring less energy would be better adapted. Thus adaptation, the process, is defined as any evolutionary change in the form-function complex which reduces the amount of energy required by the organism to maintain successfully the synerg of the stated adaptation.

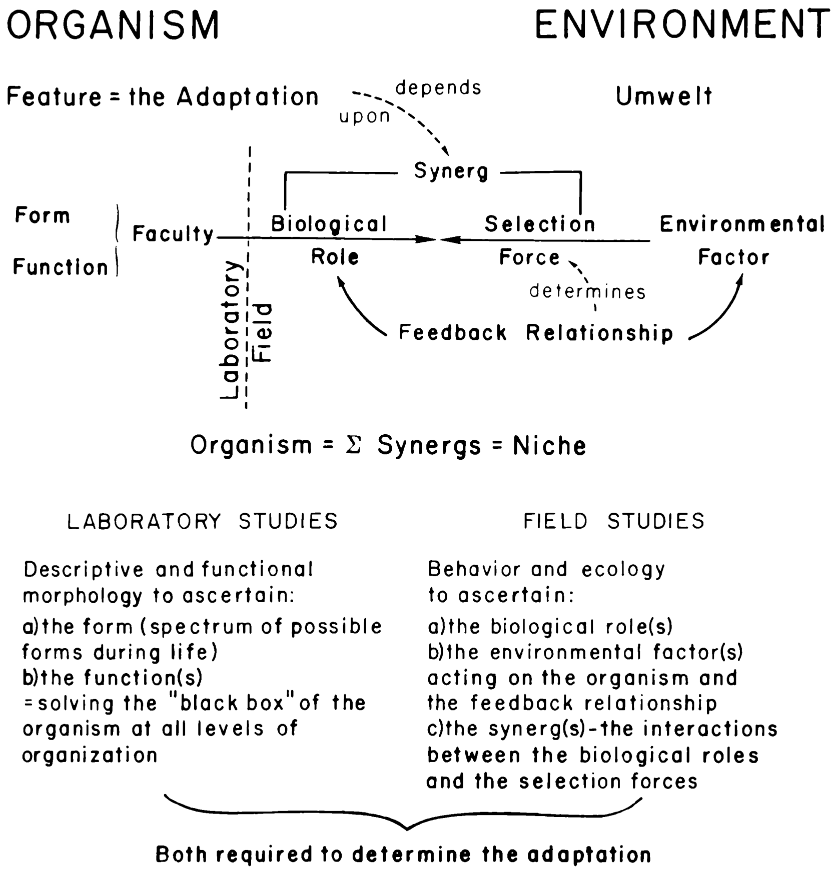

Fig. 1: Simplified scheme to illustrate the laboratory and field studies required for the direct analytic determination of an adaptation. The adaptation is the feature and is reflected in the details of its form-function complex or faculty. The existence of an adaptation is dependent upon a synergical interaction between a biological role and a selection force. A feature may represent a single adaptation or a number of adaptations depending upon the number of synergical relationships between that feature and the umwelt of the organism. In the latter case, the form of the feature and hence its functions (i. e., the properties of the adaptation) may represent a compromise between conflicting selection forces. Additional investigation is needed to ascertain (measure) the degree or the goodness of the adaptation.

The use of energy requirement to maintain the synerg as the measurement of the degree of adaptation is at least theoretically possible for any adaptation, and could be done at present for most structures of the skeletomuscular system, for example[1]) The value of an independent measure of the degree of adaptation is that it can be measured independently of other evolutionary concepts such as fitness of the individual or survival of the species. If adaptation can be measured independently, then the contribution of the adaptiveness of a feature to the fitness of an individual or to the survival of the species can be ascertained. Questions, such as if an individual possesses a better adapted feature, will it have a greater fitness?, and how close is the correlation between the degree of adaptation and fitness?, can be answered only with an independent measure of the degree of adaptation.

---

[1]) Certain problems exist in the use of energy requirements to measure the degree of adaptation because this measure does not work in all cases. It is possible to provide examples in the skeletomuscular system in which one particular form- function complex is better adapted than another even though it would

Problems and proposals for future studies in ecological morphology

Analysis of the form-function complex and its synergistic relationship to the environment makes it clear that a broad range of biological studies is needed for the determination of particular adaptations. None can be omitted and none can be done superficially. A survey of earlier studies of avian anatomy and adaptation reveals that the adaptive significance of very few features of birds have actually been shown. Most morphological studies present a detailed anatomy and, more frequently in recent years, a good functional analysis of features, but fail to include any observations of biological roles or of ecological factors. On the other hand, many ecological-physiological studies present thorough investigations of the ecological and physiological (actually a combination of functions and biological roles) factors and show what the adaptation must do, but stop short of identifying a particular feature as the adaptation and demonstrating its properties of form and function. So few complete studies exist that it is difficult to formulate any generalizations on methods.

The central problem is how can the wide range of laboratory and field studies needed to demonstrate an adaptation be done most efficiently — the question is not what must be done, but how can this be done best. I do not believe that the needed studies can be carried out by a single investigator because of the extremely broad training needed to undertake all facets of analysis. Nor does analysis of adaptations seem amenable to investigation by formally constituted research teams, at least not at this stage in our understanding. The most feasible approach appears to be by informal, flexible, small teams which divide the work between laboratory analysis of descriptive and functional morphology and field investigations of biological roles and ecological factors.

Information from both partners is needed to ascertain the nature of the synerg and of the adaptation. These teams can be set up for each individual study, but should be established as close to the beginning of the study as possible. Most fundamental to these team studies is a continuous interchange of ideas and information to permit feedback between the several major facets of the study. Each project should be integrated from the onset, not done as separate discrete studies to be put together at the end when the manuscript is written. Continuous feedback is needed because frequently, indeed probably always, essential clues are provided by the field studies to aspects of descriptive and functional morphology that must be investigated and vice versa. The nature and consequences of the feedback between the several workers in an adaptational study will be of particular concern in the examples to be presented.

Study of form. The tradition of descriptive morphology is so strong and the established bulk of published descriptive anatomy is so great that one might conlude that few problems exist in this part of adaptational study. Not quite true. Perhaps fewer problems exist in descriptive morphological study, than in other aspects of adaptational study, but not few problems. Three points may be mentioned.

a) Not only must the descriptive morphology be done with care, but with an understanding of which aspects of the structure must be described for the further functional and ecological work. Much of the existing descriptive morphology had been done with the goals of classical comparative anatomy and phylogenetics in view. Relatively little of this material is directly applicable to functional or ecological morphology (see Bock 1974: 124—126) because the morphological properties studied do not relate to pertinent functional or ecological factors.

---

require more energy. Or to show examples of adaptive changes in a form-function complex that requires more energy. A simple example would be the length of muscle fibers within a muscle — longer fibers are needed if the muscle must shorten over a greater distance. Hence, if the selection force demands that the structure, e. g., the tongue of a woodpecker, be moved over a longer distance, then a longer fibered muscle would be better adapted. But a longer fibered muscle would require more energy when it contracts and shortens. In some cases, especially those adaptations associated with feeding, these difficulties could be overcome by regarding the degree of adaptation in terms of the energy acquired by the organism compared to the energy required; indeed such a measure is used by some ecologists. However, such a ratio would not work for all features and additional study is needed to develop a more comprehensive measure of the degree of adaptation. It does seem justified, however, to use the inverse relationship between energy requirement and the degree of adaptation in the large number of cases where it appears applicable. The ratio of energy obtained to energy cost can be used for judging the degree of adaptation associated with feeding. However in other cases some objective system of measure is needed to judge the benefit to the organism to be used in ratios of benefit obtained to energy cost for ascertaining the degree of adaptation.

b) Perhaps the most unfortunate trend in the modern development of functional morphology is the lack of proper anatomical description of the systems under study. The result can almost be described as an emergence of excellent functional analyses of morphological black boxes. A major exception to this grend is the work done in the Leiden school of morphology and illustrated by the recent analysis of the filter-feeding mechanism of the mallard by ZWEERS and his associates (ZWEERS 1974, Zweers et al., 1977).
c)Lastly it must be emphasized again that features do not necessarily have one form as exhibited by the specimen under study, but almost always possess a spectrum of forms. Feathers wear, bones modify slowly as mechanical stresses alter, muscles lengthen and shorten and so forth. Even a simple morphological variable such as the weight of the individual bird is difficult to obtain because of the great and rapid changes which may occur over a few days.

Study of function. Functional morphology has been the area of active research in vertebrate anatomy for the past 30 years with the development of a modern approach to functional analysis using a variety of sophisticated tools (ALEXANDER 1968, 1975, Gans 1972, Nachtigall 1971). This development has a significant, but not sufficient part in our understanding of biological adaptations. Work has progressed furthest in analyzing the mechanisms of the skeletomuscular system of many levels.

Many examples could be cited of problems associated with functional analysis; however, these would be a repeat of material presented in my chapter on „The Avian skeletomuscular system“ (BOCK 1974) to which the reader is referred. Of the topics not covered in this paper, two significant ones should be mentioned. One is that of levels of organization in biological systems which is indirectly alluded to in the discussion on musculature. A good treatment of this topic and its pertinence to morphology and adaptation is not available. The second is the analysis of complex muscle-bone systems, e. g., the hind limb, the feeding apparatus, which was not included because of the few experimentally based studies of complex systems in birds. DULLEMEIJER (1974) has discussed these problems under the heading of holistic approaches to morphology and ZWEERS (1974, 1977) has presented an elaborate investigation of the straining habit (filter feeding) in the mallard; the last two papers should be studied as an example of the work required for a thorough functional analysis. Much additional word is needed in functional analyses of complex muscle-bone systems because the adaptiveness of individual anatomical features depends upon their contribution to the working of complete systems such as the wing or the feeding apparatus.

Study of biological roles and ecological factors. Little can be offered here because of the smaller number of studies done in ecological morphology which consider the morphology of the possibly adapted features in some detail and because of my lack of knowledge in these areas. Problems in these fields of inquiry are best treated below in the several examples of actual studies. A few points may be mentioned.

Although the definition of biological role specifies the use of a faculty by the organism living freely in its normal environment and final observations of biological roles must be made in the field, a considerable amount of the actual study may be made on captive animals. Clues to the possible biological roles are frequently obtained from the functional analysis part of the feedback between different segments of adaptational study.

Moreover many of the detailed observations are best done on captive individuals held in conditions close to natural ones. This approach permits close observation, the use of high-speed motion pictures and other rechniques difficult to employ under field conditions. LEISLER (1975, 1977) used this technique in his investigation of locomotion and perching in several species of reed warblers (genera *Acrocephalus* and *Locustella*). The comparative approach used by LEISLER is also valuable because the similarities and of contrasts between closely related species often clarify biological roles in individual species.

Case studies. Approaches to behavioral and ecological aspects of ecological morphology can be discussed best with the aid of several examples. These have been chosen to illustrate a range of problems and potential results. Special attention will be given to the consequences of feedback, or lack thereof, between the laboratory and field studies. Morphological and other details will be omitted; these can be found in the original publications.

a) Winter food storage: The Gray Jays *(Perisoreus)* possess a pair of large mucus secreting salivary glands which is as well developed as the picorum gland of the woodpeckers (BOCK 1961). No information was available on the possible functions and biological roles of the mucus. By analogy to the woodpeckers, I suggested that the sticky mucus coated the tongue which could be used as a limestick to obtain food from crevices during the winter. Dow (1965) tested this suggestion using captive jays and disproved it. He observed the birds forming food pellets, using the mucus to glue pieces of food together and then to glue the food bolus to perches and uprights of the cage. Earlier reports in the literature had described Gray Jays handling food in their bill until it was covered with a white froth (= mucus). Dow showed that the jays stored food in these boli and that the birds found and ate them when food was withheld. Subsequently, similar food boli were found attached to twigs in forests inhabitated by Gray Jays. Dow suggested that these birds stored food in the form of boli glued to branches during the winter and used this food during periods of bad weather. Thus, as he suggested, the large mucous glands are an adaptation for periods of adverse winter weather when food is scarce, being part of the food storage mechanism.

In this case the combination of two separate studies, a laboratory morphological and a behavioral-ecological study, solved the adaptiveness of the large salivary gland in *Perisoreus.* It showed that a reasonable hypothesis on the biological role of this feature obtained by analogy was wrong and that the real biological role would have appeared as a wild guess at the time of the original morphological description. This approach, although it provided a solution to the question of adaptiveness of the enlarged salivary gland in *Perisoreus,* is inefficient because of the lack of feedback between the laboratory and field studies. None existed for the morphological description, but did for the behavioral-ecological analysis. In this case, the lack of feedback did not adversely affect the laboratory study because of the relatively simple morphology and function.

b) Cross-billed drepanidids: The Hawaiian honey-creepers exhibit a wide range of bill forms and feeding methods, but the most unique member of this family is the small *Loxops coccinea.* This bird has a small finch-like bill which appears normal except that the tips of the rhamphotheca are crossed (Richards & Bock 1973). Moreover, the tips are asymmetrical in cross-section with a thin sharp edge on the crossed side. The skull exhibits little asymmetry except for the mandibular articulation. However, most jaw muscles are strongly asymmetrical but in opposite directions for the dorsal and the ventral adductors resulting in a large lateral force compenent in the direction of the asymmetry of the crossed bill tips.

A functional analysis of the jaw apparatus suggested that feeding methods involved some sidewards movement of the mandible and a strong resistance to lateral forces acting on the bill tips. And the asymmetrical sharp edges of the tips suggested some cutting or slicing action.

Richards had made extensive field observations on the feeding behavior and food of *Loxops,* including *L. coccinea,* prior to the morphological description of the feeding apparatus. At the time he was unaware of the extensive asymmetry of the mandibular articulation and jaw muscles and was not aware of the need to observe twisting or lateral motions of the head during feeding. Suggestions were offered on possible biological roles of the described asymmetry which are in agreement with the field observations made by Richards. Unfortunately no observations have been made to date which confirm or deny the hypotheses offered by Richards & Bock. Although one author (Richards) undertook both the field and the laboratory studies, the needed feedback did not exist because the field work was done before the morphological description and knowledge of the extensive asymmetry. No opportunity existed to conduct further observations of the feeding habits of *L. coccinea* in the field. Thus it is not possible to ascertain the adaptiveness of this peculiar asymmetrical feeding apparatus.

c) A two-hinged jaw: A unique jaw articulation is present in *Melithreptus* and several other genera of the Meliphagidae between the dorsal rim of the mandibular ramus and the ectethmoid plate (Bock & Morioka 1971). In *Melithreptus,* the ectethmoid articulation is formed by a distinct dorsal process of the mandible inserting into a ventral fossa of the ectethmoid. This articulation serves as a brace for the mandible when it is in the fully adducted position; it transmits from the mandible to the brain case the reaction forces of the muscles holding the mandible in place. The quadrate, freed of these reaction forces, is able to swing foreward, permitting the bird to raise its upper jaw with less muscular force.

We suggested that this ectethmoid brace of the mandible was part of a complex feeding mechanism involving the frilled tongue and a large mucous gland opening just behind the tip of the upper jaw. The mucus covered lingual frill is used, in our hypothesis, to lap up minute insects. Although several Australian ornithologists, and one of us (Bock, subsequent to publication of our morphological description) attempted to observe these birds feeding to test ideas on the possible biological roles, none were successful. Thus we still do not know the biological roles of the ectethmoid brace and cannot determine the adaptive significance of this unique jaw articulation in the Meliphagidae.

d) A sublingual shopping bag: Nutcrackers *(Nucifraga)* collect and store nuts in the ground for future consumption. In the early stages of his study of the behavior and ecology of nut harvest and storage by the Clark's Nutcracker *(N. columbiana)*, BALDA asked Bock if he would describe the morphology of the sublingual pouch. The resulting study (BOCK, BALDA & VANDER WALL 1973) showed that the large sublingual pouch does not interfere with normal tongue action, that the empty pouch is folded between the tongue apparatus and a superficial layer of muscles, and that filling of the pouch did not prevent feeding and calling of the bird. The pouch could be shown to be an adaptation for increased efficiency of harvesting nuts as the bird could collect a larger load of seeds before flying from the gathering areas to storage areas high on mountain slopes. Food storage is an adaptation for early breeding when most of the ground is still snow covered and food is scarce.

The most significant aspect of this study is that the descriptive laboratory morphology and the behavioral-ecological observations were done simultaneously with continuous feedback between the two groups of workers. Questions arising from the morphological description, such as how the pouch is emptied in the absence of sufficient muscles to do so, could be answered quickly by field observations, and vice versa. The ability to check back and forth between laboratory and field studies permitted a full analysis of all factors needed to ascertain the adaptiveness of the sublingual pouch in the nutcrackers. Neither worker, alone, could have done the entire study efficiently because of the extensive training needed and, in part, because of the need to observe nutcrackers in the field for much of the yearly cycle. Although not all problems associated with the adaptiveness of the sublingual pouch and of the food-gathering behavior of the nutcrackers were answered by this study (e. g., no experimental analysis of the function of the musculature was done, nor were the salivary glands examined in any detail), it represents, in my opinion, the ideal approach to studies of adaptation of morphological features. Information from the ecological aspects were combined continuously with that from laboratory study of the morphology to result in a biological anatomy of the type envisioned by HANS BÖKER some four decades earlier.

Acknowledgements

I would like to thank Drs. Gerd von Wahlert, Bernd Leisler and Hans Winkler with whom I discussed ideas included in this paper; their comments helped to clarify several obscure points. The various studies which formed the foundation of this analysis of ecological morphology were done with the assistance of several research grants from the National Science Foundation. Completion of this manuscript was done with support of grant BMS-7306818 from the N. S. F. which is gratefully acknowledged.

Zusammenfassung

Deskriptive und funktionelle Anatomie haben in ihrer Tradition als Laborwissenschaften viele Aspekte biologischer Strukturen, besonders die unmittelbar (proximate) bedingten, erklären können. Für die Aufklärung evolutionsbiologischer Fragen nach den mittelbaren (ultimate) Ursachen der Ausgestaltung von Strukturen und Anpassungen, die Morphologen zentral interessieren, sind sie unzureichend. Die Erkenntnis, daß die bisherige morphologische Tradition mittelbare Ursachen biologischer Strukturen nicht befriedigend erklären kann, steht im Gegensatz zur allgemeinen Auffassung der meisten Morphologen, daß ihre Methoden und Ansätze für die Klärung solcher Probleme ausreichen.

Ein volles Verständnis morphologischer Strukturen kann nur erzielt werden, wenn öko-ethologische Feldstudien und historische Aspekte die bisherigen beschreibenden und funktionsmorphologischen Untersuchungen ergänzen. Eine derartige Disziplin „Ökomorphologie" muß entwickelt werden. Die Bedeutung der Ökomorphologie kann in Verbindung mit den Methoden gesehen werden, mit denen Anpassungen analysiert werden. In einer früheren Arbeit (BOCK & VON WAHLERT 1965) wurde gezeigt, daß eine Anpassung ein Form-Funktions-Komplex eines Merkmals ist („faculty"), der in Wechselwirkung zu einem Selektionsdruck eine bestimmte biologische Rolle erfüllt, und daß Anpassungen immer im Hinblick auf bestimmte Umweltfaktoren beurteilt werden müssen. Eine Anpassung erlaubt einem Individuum erfolgreich eine Wechselbeziehung („ synerg") mit einem Umweltfaktor aufrecht zu erhalten, so daß es überlebt und sich fortpflanzen kann. Der Grad einer Anpassung kann gemessen werden. Er ist dem Energieverbrauch entgegengesetzt, den der Organismus zur erfolgreichen Aufrechterhaltung der Wechselbeziehung („synerg") benötigt.

Die Bestimmung der adaptiven Eigenschaften einer biologischen Struktur erfordert eine Kombination von Laboranalysen von Form und Funktion und Felduntersuchungen der biologischen Rolle der Struktur und der Selektionskräfte der Umwelt. Der Anpassungswert erst weniger Merkmale von Vögeln wurde bisher bestimmt, da noch kaum beide Aspekte berücksichtigt wurden. Der geeignetste und effektivste Ansatz für die Bestimmung von Anpassungen ist eine informelle Zusammenarbeit eines deskriptiven Morphologen bzw. Funktionsmorphologen mit einem Ethoökologen. Dauernde Rückkoppelung von Ideen und Informationen zwischen den beiden Bearbeitern von Beginn der Untersuchung an steigern deren Erfolg. Ein weiterer erfolgversprechender Weg bei der Analyse biologischer Strukturen liegt in evolutionsbiologischen Untersuchungen, die sowohl die traditionelle Labormorphologie wie Ökomorphologie umfassen. Für die Zukunft einer derartigen breiteren, allgemeinen Morphologie haben biologische Stationen wie die Vogelwarte Radolfzell eine wesentliche Bedeutung.

References

Alexander, R. McN. (1968): Animal mechanics. Sidwick and Jackson, London, (Also Univ. Washington Press, Seattle). ● Alexander, R. McN. (1975): Biomechanics. Chapman & Hall, London, (Also J. Wiley & Sons, New York) Outline Studies in Biology, 62 pp. ● Bock, W. J. (1959): Preadaptation and multiple evolutionary pathways. Evolution, 13: 194—211. ● Ders. (1961): Salivary glands in gray jays *(Perisoreus).* Auk, 78: 355—365. ● Ders. (1969): Comparative morphology in systematics. In Systematic Biology, Publ. 1692, Nat. Acad. Sci., Washington, D. C., pp. 411—448. ● Ders. (1974): The avian skeletomuscular system. In, Farner, D. S. and J. R. King, eds., Avian Biology, Acad. Press, New York, vol. 4: 119—257. ● Ders., In Press: Adaptation and the comparative method. ● Bock, W. J., & H. Morioka (1971): Morphology and evolution of the ectethmoid-mandibular articulation in the Meliphagidae (Aves). J. Morph. 135: 13—50. ● Bock, W. J., & G. v. Wahlert (1965): Adaptation and the form-function complex. Evolution 19: 269—299. ● Bock, W. J., R. P. Balda & S. B. Vander Wall (1973): Morphology of the sublingual pouch and tongue musculature in Clark's Nutcracker. Auk 90: 491—519. ● Böker, H. (1935—1937): Einführung in die vergleichende biologische Anatomie der Wirbeltiere. G. Fischer, Jena, 2 vols, xi + 228, xi + 258 pp. ● Davis, D. D. (1949): Comparative anatomy and the evolution of vertebrates. In, Jepsen, Simpson and Mayr, eds., Genetics, Paleontology and Evolution. Princeton Univ. Press, Princeton, N. J., pp. 64—89. ● Dohrn, A. (1875): Der Ursprung der Wirbeltiere und das Prinzip des Funktionswechsels. Leipzig. ● Dow, D. D. (1965): The role of saliva in food storage by the Gray Jay. Auk 82: 139—154. ● Dullemeijer, P. (1974): Concepts and approaches in animal morphology. Van Gorcum, Assen, 270 pp. ● Gans, C. (1972): Biomechanics. An approach to vertebrate biology. Lippincott, Philadelphia, x + 261 pp. ● Gould, J. (1973): The shape of things to come. pp. 401—404. Introduction to symposium on „Evolutionary development of form and symmetry." Syst. Zool. 22: 401—506. ● Leisler, B. (1975): Die Bedeutung der Fussmorphologie für die ökologische Sonderung mitteleuropäischer Rohrsänger *(Acrocephalus)* und Schwirle *(Locustella).* Journ. f. Ornith. 116: 117—153. ● Ders. (1977): Die ökologische Bedeutung der Lokomotion mitteleuropäischer Schwirle *(Locustella).* Egretta 20: 1—25. ● Mayr, E. (1961): Cause and effect in biology. Science, 134 (3489): 1501—1506. ● Ders. (1972): The nature of the Darwinian revolution. Science, 176: 981—989. ● Nachtigall, W. (1971): Biotechnik. Quelle &Meyer, Heidelberg. Uni Taschenbuch 54, 127 pp. ● Richards, L. P., & W. J. Bock (1973): Functional anatomy and adaptive evolution of the feeding apparatus of the Hawaiian honeycreeper genus *Loxops* (Drepanididae). A. O. U. Ornithol. Monogr. 15, x + 173. ● Russell, E. S. (1916): Form and function. A contribution to the history of animal morphology. John Murray, London, ix + 383 pp. ● Young, J. Z. (1950): The life of vertebrates. Oxford Univ. Press, Oxford (2nd ed. 1962, xv + 829 pp.). ● Ders. (1957): The life of mammals. Oxford univ. Press, Oxford, xv + 820 pp. ● Zweers, G. A. (1974): Structure, movement, and myography of the feeding apparatus of the mallard *(Anas platyrhynchos* L.). Neth. Journ. Zool., 24: 323—467. ● Zweers, G. A., A. F. C. Gerritsen & P. J. van Dranenburg-Voogd (1977): Mechanics of feeding of the mallard *(Anas platyrhynchos* L.). The lingual apparatus and the suction-pressure pump mechanism of straining. Contr. Vert. Evol. vol. 3: 88. S. Karger, Basel.

Anschrift des Verfassers: Professor Dr. W. Bock, Department of Biological Sciences, Columbia University, New York, N. Y. 10027, U.S.A.