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Topics in Functional and Ecological Vertebrate Morphology: Introduction

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Functional and Ecological Morphology?

Presenting a miscellaneous compilation of papers under the common cover 'Topics in Functional and Ecological Morphology' might be somewhat puzzling at first. On the one hand, such a title suggests a close connection between functional and ecological morphology. On the other hand, it emphasises the distinct nature of both 'disciplines'. In this short introduction we want to argue that this twofold interpretaton of the title is indeed justified. Once denoting separate disciplines, functional and ecological morphology now rather tend to refer to consecutive, practical steps in an integrated evolutionary research program. However, methods still differ considerably.

Unravelling the relationship between an organism's appearance and the way it performs ('functions') in its environment is the fundamental aim of both functional and ecological morphology. Since no biologist can neglect the shaping role of natural selection in evolution, this aim largely boils down to the desire to grasp the process of adaptation. Yet, the link between the phenotypic variation and environmental diversity is not always obvious or straight forward, especially when focusing on lower taxonomical levels. Constraints may slow down or obstruct the process of natural selection (e.g. Maynard Smith et al., 1985), and obvious correlations between certain phenotypic and environmental traits can be non-adaptive. Therefore, meeting this desire asks for a rigorous integrated approach in which functional and ecological morphology both fulfil an essential role.

Arnold (1983) offered the basic conceptual frame-work for a such a proper analysis (see also Aerts et al., 2000; Van Damme et al., 2002). Measuring the degree to which individual organisms can fulfil (aspects of) ecologically important functions (e.g. biting, singing, sprinting, manoeuvring…) takes a central position in this. On the one hand, the causal link between this variation in performance and the variation in biological fitness should be understood. On the other hand, it must be investigated how this variation in performance is related to phenotypic variation, and it must be determined whether or not a genetic basis for that variation exists. It is tempting, but imprudent, to assume that correlations between the successive stages in this research program (genotype, phenotype, performance and fitness) denote causal links. It is here that functional and ecological morphology enter the analysis of adaptation.

Phenotypic variation and performance

Understanding how phenotypic variation translates (or does not translate) in differential performance requires *function analysis*, either through experimental work or via mathematical modelling. The mechanism behind the link needs to be discovered. Establishing, for instance, that faster specimens (or species) have longer limbs does not suffice to conclude that they are faster *because* they have longer limbs. Maybe, the long limbed specimens always run 'groucho' (cf. McMahon et al., 1987; with bent hips, knees and ankles), thus reducing the effective length of the

limbs. In that case, high running speeds will result from higher cycling frequencies, rather than from longer strides or steps. This can only be determined when a kinematical analysis is carried out, a type of analysis typically attributed to the domain of functional morphology.
It should be noted that phenotypic variation is much broader than variation in morphology alone. In the example above, the variation in running performance might be due to biochemical (e.g. enzyme activity) or physiological differences (e.g. VO_2max), rather than purely morphological ones. Obviously, a complete understanding of the performance gradient will require functional analyses beyond the traditional field of functional morphology. Several chapters in this book illustrate how functional morphology and physiology are currently blending into an integrated system approach of organismal perfomance.

Performance variation and fitness
Unravelling the causal relationship between performance and fitness is, in many cases, even more problematic and requires additional *ecological analyses* to evaluate the ecological relevance of the trait considered. First, performance measures obtained from laboratory experiments should be confirmed under natural circumstances. For instance, animals running very fast on a race track in the lab might perform differently in nature simply because the structure of their habitat does not allow to attain high speeds. In this case, speed would be ecologically irrelevant (i.e. it plays no role in the fitness of the organism) and the high level of performance is, for instance, a 'historical' remain or a consequence of another adaptation. Secondly, behavioural observations under natural circumstances must confirm the ecological relevance of the function studied. Negative effects on fitness by decreased performance can be compensated for by altered behaviour. Being ignorant of such behavioural compensation will lead to the wrong conclusions.

Hence, functional morphology and ecological morphology can be considered as consecutive steps in the same integrated evolutionary research program. Through the specificity of these steps, however, both approaches appear to differ considerably.

- *Ecological morphology* puts the focus primarily on the 'performance - ecology' link. Although 'form'-variation is considered, there is no explicit emphasis on its mechanistic link with performance. Morphometrics, performance measurements, eco- and ethological observations, field work, etc., form part of the proper ecological morphological analysis. Add quantitative genetics and fitness measurements to this and the entire evolutionary research program is realised. Comparison of large numbers of specimens and/or species is intrinsic to this kind of analysis and conclusions mostly build upon inductive reasoning and (statistical) modelling.
- *Functional morphology* focuses on the 'form - performance' link. Gaining insight in the precise way in which biological machinery performs under relevant conditions is of primary importance. Detailed morphological and morphometric study, movement analysis, dynamographics, electromyographic recordings, registration of physiological processes (like measuring respiration rates…), performance measurements, etc, all belong to the functional morphological repertoire. Of course, functional morphology does not reject comparison, but the intensity of the in-depth analysis and intricacy of many of the techniques often hinder a broad comparative experimental set-up. Consequently, many studies focus on very specific 'how, what and why' questions. New hypotheses on adaptation and evolution are formulated afterwards, by expanding the results of the functional morphological analysis (deductive reasoning). This is often done through mathematical modelling.

There is no doubt that disputes between both 'disciplines' will continue. Some ecological morphologists will continue to criticize the seeming lack of adaptive reasoning in functional morphology, and some functional morphologists will always deride functional analyses in 'ecological' studies as being superficial. However, the fortunate fusion between functional and ecological morphology is ongoing and cannot be turned back. Both approaches clearly complement each other and are of immense value for the integrative research program in biological evolution.

About this book

This book is a tribute to Professor Frits De Vree of the Laboratory for Functional Morphology at the Department of Biology of the University of Antwerp (Belgium). In 1973, Frits started to build the first experimental biology lab for functional morphological research in Flanders. About 30 years later, upon his retirement, this lab is not only still unique in Flanders, but has also gained world-wide scientific recognition.
At the occasion of the retirement of Frits De Vree, we decided to organise a symposium that covered topics related to those tackled in the Functional Morphology lab. Members of the lab in Antwerp have studied musculo-skeletal function in all vertebrate classes (including humans) over the past 30 years. During the last decade of Frits' career, the fusion between functional and ecological morphological approaches mentioned above was further enforced in Antwerp by formally merging two research groups already collaborating for a while. Based on these historical arguments, it was decided to entitel the symposium: *Topics in Functional and Ecological Vertebrate Morphology - A Tribute to Frits De Vree.*
The invited contributions of this symposium, together with seven other invited chapters are compiled in this book. They are all written by scientists who know Frits De Vree very well. With this compilation, an effort is made to cover the wide range of research topics, study objects, approaches and concepts dealt with in the lab during Frits' career. The chapters were all peer-reviewed. In light of the argument presented above, the chapters are arranged along a continuum from functional morphology, over ecological morphology towards evolutionary biology and finally contributions on methodological approaches and theoretical concepts.

One word about the cover picture. For years, *Gekko gecko* was Frits' favourite study object. He painstakingly studied the anatomy and histology of the head of this lizard through macroscopic dissections and microscopical serial sections. Three dimensional movement patterns during feeding were analysed by means of high speed film and cineradiography. Simultaneously, electromyograms of all head muscles were recorded and contraction characteristics of several important head muscles were obtained. In other words : this study could be a paradigm for functional morphological research. Unfortunately, his many duties in the university community prevented Frits from publishing this immense work. We hope that, now his 'active' scientific management career has come to an end, he will finally find the time and joy to finish that job.

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