

Science as a Way of Knowing—Evolution: The Biology of Whole Organisms¹

MARVALEE H. WAKE

*Department of Zoology and Museum of Vertebrate Zoology, University of California,
Berkeley, California 94720*

SYNOPSIS. Examples of current research of importance to the conceptual and informational bases of evolutionary biology in the areas of morphology, development, physiology, ecology, population biology, natural history, and systematics are discussed. A synthetic approach to problems that utilizes ideas and techniques from several areas of biology characterizes much current research, and it is providing new conceptual frameworks and new, testable hypotheses. Some of the possible problems with methods of presentation as we often teach in these areas of biology are considered.

The conceptual and informational bases of evolutionary biology continue to be strengthened through current research. Investigations of the biology of organisms, their relationships, and their interactions with the environment add to our understanding of pattern and process of evolution; indeed, science is a way of knowing.

The charge to suggest important current events in virtually all areas of organismal and supra-organismal biology that enhance our knowledge of evolution is a broad one, incredible in the literal sense of the word. At risk of having my sanity questioned, I accepted the charge when it occurred to me that each of us, when we design a course, faces that same task. Because of the breadth and diversity of morphology, development, physiology, behavior, ecology, population biology, systematics, and natural history, and in accord with constraints of space and time, I shall limit my comments to a few selected examples in these areas, especially emphasizing their contributions to new conceptual frameworks. I shall also note some other topics of current research interest, and comment on some of the problems with methods of presentation, as I perceive them. These comments are meant as suggestions, or possible guidelines.

I encourage you not to aggregate these examples in a "unit on evolution" within

a course, but to use them to emphasize the concept of evolution as pervasive to our knowledge of biology. Biology is too often divided into "how it works" and "how it has come to work" halves, and it is most important that they be integrated, and focused on whole organisms. The examples I have selected can be treated in many different contexts, and in fact their unifying theme, along with evolution *per se*, is that each represents a synthesis of ideas and techniques from several areas of biology. This synthetic approach characterizes current research in all of the areas of biology that I have examined, and it is providing new conceptual frameworks and new, testable hypotheses. These ideas and examples can be presented at different levels of complexity and detail, so I shall risk giving too much information on some topics and too little on others for your various possible uses. These suggestions, which I hope provoke other ideas, can be amplified or generalized as appropriate to your courses and teaching styles.

MORPHOLOGY AND DEVELOPMENT

We often teach morphology, when we teach it at all in a first year course, in a highly typological way, selecting only a few examples. Morphology, I suspect, is most often presented in the context of animal and plant diversity, and I fear that students often come away from that exposure with a sense of the immutability of form, rather than of diversity and variation. Further, development is often presented, in both texts and lectures, as a study of regulation

¹ From the Symposium on *Science as a Way of Knowing—Evolutionary Biology* presented at the Annual Meeting of the American Society of Zoologists, 27-30 December 1983, at Philadelphia, Pennsylvania.

of processes that occur very early in the establishment of organisms, and development "stops" pedagogically with neurulation. Organogenesis and particularly the concept of ontogeny are not often dealt with, leaving students with little connection between "development" and "morphology."

However, recent work, much of it employing principles and techniques from both fields, has provided a new conceptual framework for understanding mechanisms and patterns of morphological change and diversification, constraints on size and shape, and the biomechanics of organisms. This emphasis is changing our understanding of the morphological changes that we see following speciation, as well as some aspects of the speciation process, and our assessment of the patterns of origins of major groups. Three examples illustrate this synthetic research.

In 1979, Alberch *et al.* presented a formalization showing how small changes in timing and rates during development might effect significant changes in morphology. In other words, quantitative changes in basic parameters of development can result in qualitative changes in morphology, and such perturbations are responsible for transitions among morphological body plans (Alberch, 1982). Alberch has argued that changes in body plan are constrained by the structure of postulated developmental programs, so he determined to test experimentally these ideas. Among both frogs and salamanders, there are numerous examples of species within lineages with different numbers of toes. Assuming that pentadactyly is primitive, the questions are: which toes are lost, in what sequence, and by what mechanism? Alberch and Gale (1983) devised a simple but elegant experiment to answer these questions. They treated limb buds on one side in a frog, *Xenopus laevis*, and a salamander, *Ambystoma mexicanum*, with the mitotic inhibitor colchicine and allowed development then to proceed. The treated limbs were smaller and had lost skeletal elements compared to the contralateral controls. Further, frogs always lost the first toe, salamanders the fifth. These differences then are correlated

with qualitative differences in developmental sequence of digital differentiation in frogs *vs.* salamanders. Colchicine administration temporarily arrests mitotic divisions resulting in fewer cells and a smaller limb bud. This developmental retardation and reduced cell number result in a digital loss. Therefore, this is a continuous process (reduction of rate of cell division) with a strongly discontinuous outcome (loss of an entire digit, of many parts). It can then be inferred that a slight perturbation in developmental pattern could, assuming heritability and in concert with selection, effect a major morphological difference with long-range consequences. Slight differences in developmental programs and epigenetic regulatory mechanisms may be fundamental to morphological differentiation within lineages.

In addition to developmental and phylogenetic constraints on possible sizes and shapes, there are mechanical limits as well. The properties of the materials of which organisms are composed confer these limits, and design constraints are thus inherent. Trees are effectively towers that are open networks of cantilevered beams (stems and branches) that support many solar collectors (leaves) (Wilson and Archer, 1979). The problem is that trees grow, in contrast to engineers' towers. Beams get longer and thicker and produce new beams by branching. Beams (branches) are subject to bending and torsional stresses from the loads of self-weight, wind, etc. As the tree grows these forces increase, so the beams are stiffened to resist the forces against them. Different species have different leaf distributions and designs, and branching patterns, hence design is flexible enough to meet specific mechanical requirements. Strain stimuli affect rate of cell production, gravitational stimuli affect microfibril angle and internal strain; these are feedback systems. Wood rays in a tree limb are located so that they can sense strain in branches. McMahon (1975) demonstrates that these elastic criteria impose limits on biological proportions, and therefore metabolic rates in both plants and animals. Trees too tall and/or slender would be subject to buckling or compression. If branches are to

effect maximum lateral displacement from trunk so that leaves are exposed to light, there is also a point at which the length/weight ratio of a limb would cause bending toward the trunk. Elastic criteria in theory set length proportional to the $2/3$ power of diameter in both trunk and branches. Data on a diversity of species of trees indicate that the proportions of trees do not ever exceed this value, hence the theoretical prediction is supported. In animals shape also changes with scale. When a quadruped is standing, limbs are exposed to buckling loads and the vertebral column and its musculature to bending loads. When the animal runs, the situation is reversed, the limbs subject to bending loads and the vertebral column to buckling because of the thrust of limb propulsion. Again, length is proportional to the $2/3$ power of diameter. Surface area increases as the $2/3$ power of weight. This suggests that living organisms are required to adopt forms in which lengths increase, or scale, as the $2/3$ power of diameter. Somatic dimensions of a number of species of both plants and animals support this conclusion (McMahon, 1973). (There is nothing magic or universal about the $2/3$ ratio; other significant biological relationships scale differently.)

Finally, Gans and Northcutt (1983) and Northcutt and Gans (1983) have utilized morphological and developmental data to propose a reinterpretation of the origin of vertebrates. They point out that most of the morphological and functional differences between vertebrates and other chordates occur in the head. Further, these structures are derived from epidermal placodes, neural crest, and muscularized hypomere. The derivatives of neural crest and epidermal placodes may have arisen from the epidermal nerve plexus of protochordates. Gans and Northcutt suggest that developmental changes are associated with a shift from filter feeding to predation, and more efficient patterns of locomotion and gas exchange led to reorganization of the pharynx, with elaboration of circulatory, digestive, and nervous systems and the development of special sense organs. Epidermal placodes and neural crest form special sense organs and other

neural structures; developmental and endocrinological data support this idea (see below). It is now well known that neural crest contributes to connective, skeletal, and muscular tissue of the head. They hypothesize that electroreception developed as a means of detecting prey. Derived from epidermal placodes, electroreceptive organs were functionally enhanced by the deposition of hydroxyapatite. These deposits led to dentinous and enamel tissues to maintain the orientation of the sensory receptors, then to cartilage and bone, ossification therefore being a very late indicator of the vertebrate grade. Northcutt and Gans suggest that support tissues (cartilage, bone, dentine, enamel) arose in association with the new sensory organs, and only secondarily provided mechanical support. The development of dermal armor occurred later, and the origin of axial vertebrae and a post-otic skull (composed of vertebral segmental elements?) is associated with the development of jaws.

This is an evolutionary scenario. It provides a new way of looking at the origin of vertebrates and at a number of questions of the origin of particular structures. It also provides a number of testable hypotheses regarding both development and function, in fact, more than the authors conservatively imply. For example, Gans and Northcutt suggest that monoclonal antibodies against neural crest or placodal tissue should be able to distinguish common derivation from these sources *vs.* independent ectodermal origin, and specific biochemical markers characteristic of neural crest should also occur in placode derivatives and in protochordate epidermal nerve plexus. Inducing perturbation in development might also be instructive, as neural crest transplant work suggests. One should not take pot-shots at parts of this scenario; one should test them.

PHYSIOLOGY

Evolution can be interwoven readily into the teaching of physiology, though physiological processes are often presented in a rather mechanistic way. It is important to associate physiological processes with whole organisms, and physiology with

responses of those organisms to their environment. Current research in several areas is providing important information for biologists. Work on aerobic *vs.* anaerobic metabolism in vertebrates and invertebrates (such as that of Bennett, 1982) is becoming important to our understanding of the evolution of major groups since it indicates that metabolic "efficiency" need not be associated with endothermy. Other kinds of studies of energetics are important to understanding evolution, and also involve multiple areas of biology, such as ecology and behavior. The physiological *costs* of reproduction, of feeding, of aggression, are significant variables for our assessment of life history evolution (see Congdon *et al.*, 1982). In fact, the work of physiological ecologists, focusing on responses of organisms, plant and animal, and the evolution of those responses, such as metal tolerance in plants, is an exciting and emergent area of study. Investigations into reproductive biology, including endocrine mechanisms, oogenesis and spermatogenesis, etc., are providing useful comparative data for understanding everything from reproductive timing to aspects of reproductive isolation. I draw on data from all of these areas, and morphology, development, and behavior, as I pursue studies on the evolution of live-bearing modes, including viviparity, in all vertebrates (Wake, 1982). A diversity of data is applicable to our analysis of plasticity, a concept now receiving considerable attention among evolutionary biologists. I shall focus on one particular example as a suggestion of the way that a physiological principle (mechanism) can be presented in an evolutionary context.

Dorothy Krieger elegantly summarized the evolution of brain peptides in a recent article in *Science* (Dec. 1983). The evolutionary origins of brain peptides and of polypeptide hormones are questions of great current interest because of several recent observations: 1) peptides considered to be of glandular origin have been found in vertebrate nervous tissue; 2) peptides thought to occur only in vertebrate glandular tissue have been identified in invertebrate neurons and in unicellular

organisms; 3) peptide receptors have been found in unicellular organisms; 4) peptides previously known only in invertebrates have been found in vertebrate tissue; 5) and diverse peptides have similar sequences within and between species. Also, substances similar to hormonal peptides and neurotransmitters are present in plants and unicellular organisms. It is suggested that these peptides are primitive components of intercellular communication. Then in sponges, these messenger molecules are localized, and function as neurotransmitters. Coelenterates and annelids use peptides as both neurotransmitters and neurohormones, but lack endocrine tissue *per se*. Common brain-gut peptides occur in lampreys, and all other vertebrates. These observations suggest that so-called products of the nervous and endocrine systems were present before those systems evolved; as nervous and glandular tissues developed, the tissues expressed specific peptides previously diffuse in lower organisms. Common peptides occur in diverse tissues—hydra head activating factor, a coelenterate neuronal peptide, is present in vertebrate gastrointestinal tract and in neurons. ACTH and prolactin are present in vertebrate endocrine and neural tissue, and invertebrate neuronal tissue. Insulin occurs in vertebrate endocrine (pancreatic) tissue, but in both gastrointestinal secretory cells and neurons in invertebrates. It is also suggested that the neuronal system preceded the endocrine in an evolutionary time scale. Receptors also evolve, both in structure and in function. Prolactin in teleosts effects fluid homeostasis, but in mammals regulates secretion of mammary glands. Alpha-factor, a yeast mating pheromone, has extensive sequence homology with the vertebrate hypothalamic luteinizing hormone releasing hormone (LHRH), binds to rat pituitary LHRH receptors, and stimulates release of luteinizing hormone (LH) from cultured gonadotrophs. These observations suggest that the peptides are very old evolutionarily, and maintained throughout evolution. Further, a given peptide can act as a local factor, a hormone, a neurohormone, or a neurotransmitter in different instances, even within a

species (such as POMC, the ACTH precursor; a neurotransmitter in the brain, a hormone secreted by the pituitary, a neurohormone acting on gonadotroph function, and a paracrine factor in the reproductive and gastrointestinal tracts of certain vertebrates). In the course of evolution, then, the same peptide also may have changed function among these means of cellular communication. At any rate, this sort of research, and the synthetic view of it, give us a new framework for analyzing physiological processes, and similarity, variation, and change among organisms in an evolutionary context.

POPULATION BIOLOGY, ECOLOGY, AND NATURAL HISTORY

Work in these areas is highly complementary, often, as in areas of organismal biology, borrowing techniques and combining approaches to problems. For example, physiological ecology, already alluded to, is practiced by ecologists looking at resource use from energetic and evolutionary perspectives (Calow and Townsend, 1981). Behavioral ecology has become a synthesis of its own, as exemplified by Krebs and Davies (1978) (*Behavioral Ecology: An Evolutionary Approach*). Much of research in behavioral biology makes significant contributions to our knowledge of evolution. Analysis of such problems as coevolution—plant-animal interactions, parasite-host evolution—depends on both a conceptual framework and data drawn from application of diverse techniques. Conceptual advances have been made by introducing such ideas as game theory and the concept of the evolutionary stable strategy (Maynard Smith, 1982) and optimality theory (see discussions in Krebs and Davies, 1978; Oster and Wilson, 1978, and Alexander, 1982) in order to provide new frameworks for analysis in behavior, ecology, and life history “strategy.”

I shall consider the analysis of sexual selection as one example of current research that is providing a new conceptual and informational base for evolutionary biology. Sexual selection is selection solely in regard to obtaining mates. Darwin envisioned the process of natural selection as

giving rise to adaptations used in the struggle for existence. Later, as developed in *Descent of Man and Selection in Relation to Sex* (1871), he realized that natural selection cannot begin to explain many sexually dimorphic traits observed in nature because such traits would decrease the survival ability of the bearer; the traits are maladaptive in regard to natural selection. Therefore, he postulated the theory of sexual selection, explaining that traits which might even lead to decreased survivorship can still be selected for if they increase the ability of an animal to mate. The crucial distinction between natural selection and sexual selection, as drawn by Darwin, is that natural selection can result in the evolution of traits that increase survival ability, and sexual selection can lead to the evolution of traits that increase ability to attract mates even though they reduce survivorship. This distinction is lost when “Darwinian fitness” is defined as changes in allelic frequencies. So, Darwinian fitness is not what Darwin meant by fitness. Some have argued that the difference is semantic, since all we should be interested in is how allelic frequencies change; others have said that there is a crucial difference and the two should not be mentioned in the same breath. Regardless, the two forms of selection are processes and their modes of operation are different, and this needs to be understood.

Ryan (1983) has documented the costs and benefits of frog calls in terms of female choice of mates, effectiveness of communication, and male and female reproductive success. He and colleagues (Ryan *et al.*, 1982) also have documented the maladaptiveness of frog calls *vis-à-vis* natural selection. In *Physalaemus pustulosus*, a neotropical leptodactylid frog, the calls are a trait presumed to have evolved through sexual selection, and increase male reproductive success. However, the calls of the apparently most attractive males are also the most effective in attracting predators, thus decreasing the survival ability of the caller. In this case, sexual selection may actually oppose natural selection, and selection processes do not necessarily lead to maximization of population size, or other aspects of increase of “fitness.” Another part of

research in sexual selection is that of the evolutionary consequences of female choice in the speciation process. The basic idea is that courtship signals of different populations of the same species diverge (adaptive or random divergence); this leads to reproductive isolation between populations since on re-contact potential mates either do not recognize each other or prefer mates from the local population. Then, as a result of a lack of gene flow between populations, the genomes begin to diverge and eventually there is a lack of genetic compatibility. These ideas are discussed by Arnold (1983) and West-Eberhard (1983).

The evolution of life history traits is receiving considerable attention, for it involves study of the natural history, population biology, ecology and physiology of organisms in order to understand the nature of and effects of such parameters as clutch size, reproductive period, age at first reproduction, life expectancy, and mortality. Tuomi (1982), Ballinger (1983), Berven and Gill (1983), Kaplan (1980) and Stearns (1980, 1983) have all provided recent new analyses of the evolution of life history phenomena, and that synthetic approach is important to our understanding of the nature of variation and its implications for evolution at the organism and population levels.

SYSTEMATICS

As I see it, the problem with systematics as it is dealt with in most courses is the presentation of a static taxonomy, into which organisms are pigeon-holed in order to have names, and a hierarchical arrangement of unquestioned relationships. In fact, systematics is a dynamic part of evolutionary biology, recently utilizing new techniques and new methods of analysis. One part of systematics is the description of recognizable, discrete entities, on the basis of distinguishing characteristics. Another is the ordering of species into a system of classification, based on shared characteristics. A third part is a phylogenetic interpretation of that classification. A major question today is the degree to which the classification hierarchy represents evolutionary events: order of descent from

ancestors (the genealogy) and extent of divergence from ancestors, *i.e.*, evolutionary relationship and rate of change or divergence. Two themes pervade modern systematics—new methods of analysis of relationship, and the introduction of new techniques for assessing degree of relationship, or divergence from an ancestral stock. Systematists compare taxa, and then cluster them into groups using some similarity criterion. The three primary current methodological approaches to assigning rank, such as order or family, to units in classification hierarchies (Calow, 1983) are: 1) numerical taxonomy (phenetics, which assesses overall similarity, including both homology and convergence), 2) evolutionary or natural order systematics, which deals with genealogy and similarity and divergence with intuitive but not necessarily objective or universal rules for analysis, and 3) phylogenetic systematics (cladistics, or genealogical relationships based on shared derived characters, or homologies). Cladistics employs a rigorous methodology assessing shared derived characters to arrange related species in dichotomously branching sets. It assesses homology and polarity of characters. Pheneticists and natural order systematists first classify the taxa, then assess relationships. Cladists first reconstruct a phylogeny or genealogy of relationships of taxa, then design a classification consistent with the phylogeny (see Charig, 1982). There are strong adherents to each of these approaches. I will not go through their arguments, but it is important to let students know that systematics does not simply provide names and ranks, but it also provides an assessment of similarity regardless of descent, or an assessment of evolutionary divergence and relationship. There are different methods for illustrating these relationships. Cladograms, etc., “look different” from “Romerograms,” and students will need to know why—both exist in textbooks, often without explanation. Students are forced to intuit what they mean, but these diagrams should be presented with an explanation of their bases.

Until recently classifications were based largely on morphological data. These were

assumed to be a fairly conservative expression of phenotypic variation, and homologies were used to assess similarity and divergence. Other kinds of characters (physiological, reproductive, life history, ecology, karyotypes) fairly recently have been incorporated into analyses. However, new advances in systematics are being made via the incorporation of techniques of biochemistry and molecular biology. These include electrophoresis of a diversity of proteins, microcomplement fixation, a quantitative immunological technique that counts the number of amino acid substitutions in a given protein in compared taxa, radio-immunoassay, and DNA-DNA hybridization. These methods allow comparisons among populations and species of the data generated. These are largely techniques for assessing *genetic* similarity. Most also give insight into modes of speciation and rates of evolution. An example of the utility of these approaches is provided by the work of Charles Sibley, a systematic ornithologist, who has evaluated the taxonomic relationships and evolution of birds based on morphology, behavior, electrophoresis and now DNA-DNA hybridization. He finds that the newer techniques provide phylogenies that often corroborate those based on morphology, but also may provide new evidence for different taxonomic associations based on genetic similarity (Sibley and Ahlquist, 1981, 1982). These techniques require new methods for analysis of these data as non-morphological characters that evolve, and numerous methods have been generated that can then be used by cladists, pheneticists, or evolutionary systematists. They also provide new data sets for evaluating competing evolutionary hypotheses, be they for evolution as a process in general, or specific to a group of organisms being assessed (see Mickevich and Metter, 1983).

In summary, we cannot present all aspects of both concept and information to our students. Time constraints, and those of materials and backgrounds, dictate this. Even so, I suggest that a minor "perturbation" or our "developmental" or teaching program is appropriate. We can then use principles of evolution to provide the

conceptual basis for our teaching of *all* of the properties of organismal and supra-organismal biology throughout our courses, whether they are "general" or more specialized sub-fields of biology. This might allow students to integrate both concepts and their supporting data more efficiently than teaching a body of "facts" (which have a certain transmutability), thus reinforcing evolution as a major aspect of science as a way of knowing.

ACKNOWLEDGMENTS

I thank my colleagues George Barlow, Roy Caldwell, Harry Greene, Mark Kirkpatrick, Mimi Koehl, Robert Robichaux, Michael Ryan, and David Wake for provocative and stimulating discussions of evolutionary biology, some contained herein. David Wake critically read the manuscript. I wish to acknowledge the support of the National Science Foundation for my research and that of much current research of importance to evolutionary biology.

I dedicate this paper to the memory of Ina H. Wake; member of the first BSCS writing team, teacher (and mother-in-law) extraordinaire.

REFERENCES

- Alberch, P. 1982. The generative and regulatory roles of development in evolution. In D. Mossakowski and G. Roth (eds.), *Environmental adaptation and evolution*, pp. 19-36. G. Fischer Verlag, Stuttgart.
- Alberch, P. and E. A. Gale. 1983. Size dependence during development of the amphibian foot. Colchicine induced digital loss and reduction. *J. Emb. Exp. Morph.* 76:177-197.
- Alberch, P., S. J. Gould, G. Oster, and D. B. Wake. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296-317.
- Alexander, R. M. 1982. *Optima for animals*. Edward Arnold, London.
- Arnold, S. J. 1983. Sexual selection: The interface of theory and empiricism. In P. Bateson (ed.), *Mate choice*, pp. 67-108. Cambridge Univ. Press, Cambridge.
- Ballinger, R. E. 1982. Life-history variations. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard ecology studies of a model organism*, pp. 241-260. Harvard Univ. Press, Cambridge, Mass.
- Bennett, A. F. 1982. The energetics of reptilian activity. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, pp. 155-200. Academic Press, London and New York.
- Berven, K. A. and D. E. Gill. 1983. Interpreting

- geographic variation in life-history traits. *Amer. Zool.* 23:85-97.
- Calow, P. 1983. *Evolutionary principles*. Blackie Publ., Glasgow and London.
- Calow, P. and C. R. Townsend. 1981. Energetics, ecology and evolution. In C. R. Townsend and P. Calow (eds.), *Physiological ecology: An evolutionary approach to resource use*, pp. 3-19. Blackwell Sci. Pubs., Oxford.
- Charig, A. J. 1982. Systematics in biology: A fundamental comparison of some major schools of thought. In K. A. Joysey and A. E. Friday (eds.), *Problems in phylogenetic reconstruction*, Syst. Assn. Sp. Vol. 22, pp. 363-440. Academic Press, London and New York.
- Congdon, J. D., A. E. Durham, and D. W. Tinkle. 1982. Energy budgets and life histories of reptiles. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 13, pp. 233-272. Academic Press, London and New York.
- Darwin, C. 1871. *The descent of man and selection in relation to sex*. Random House, New York. (Rpt.)
- Davies, N. 1982. Behavior and competition for scarce resources. In King's College Sociobiology Group (eds.), *Current problems in sociobiology*, pp. 363-380. Cambridge Univ. Press, Cambridge.
- Gans, C. and R. G. Northcutt. 1983. Neural crest and the origin of vertebrates: A new head. *Science* 220:268-274.
- Kaplan, R. 1980. The implications of ovum size variability for offspring fitness and clutch size within several populations of salamanders (*Ambystoma*). *Evolution* 34:51-64.
- Krebs, J. R. and N. B. Davies. 1978. *Behavioral ecology: An evolutionary approach*. Sinauer Assoc. Inc., Sunderland, Mass.
- Krieger, D. T. 1983. Brain peptides, what, where, and why? *Science* 222:975-985.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge Univ. Press, Cambridge.
- McMahon, T. A. 1973. Size and shape in biology. *Science* 179:1201-1204.
- McMahon, T. A. 1975. Mechanical design of trees. *Sci. Am.* 233:93:102.
- Mickevich, M. F. and C. Mitter. 1982. Evolutionary patterns in allozyme data: A systematic approach. In N. I. Platnick and V. A. Funk (eds.), *Advances in cladistics*, Vol. 2, pp. 169-176. Columbia Univ. Press, New York.
- Northcutt, R. G. and C. Gans. 1983. The genesis of neural crest and epidermal placodes: A reinterpretation of vertebrate origins. *Quart. Rev. Biol.* 58:1-28.
- Oster, G. F. and E. O. Wilson. 1978. *Caste and ecology in the social insects*. Princeton Univ. Press, Princeton, N.J.
- Ryan, M. J. 1983. Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. *Evolution* 37:261-272.
- Ryan, M. J., M. D. Tuttle, and A. S. Rand. 1982. Bat predation and sexual advertisement in a Neotropical anuran. *Amer. Natur.* 119:136-139.
- Sibley, C. G. and J. E. Ahlquist. 1981. The relationships of the Accentoes (*Prunella*) as indicated by DNA-DNA hybridization. *J. f. Ornith.* 122:369-378.
- Sibley, C. G. and J. E. Ahlquist. 1982. The relationships of the Yellow-breasted Chat (*Ictera virens*) and the alleged slowdown in the rate of macromolecular evolution in birds. *Postilla* 187:1-19.
- Stearns, S. C. 1980. A new view of life-history evolution. *Oikos* 35:266-281.
- Stearns, S. C. 1983. The evolution of life-history traits in mosquito-fish since their introduction to Hawaii in 1905: Rates of evolution, heritabilities, and developmental plasticity. *Amer. Zool.* 23:65-75.
- Tuomi, J. 1982. Evolutionary theory and life history evolution: The role of natural selection and the concept of the individual organism. *Rpts. from the Dept. of Biol., Univ. Turku* 4:1-14.
- Wake, M. H. 1982. Diversity within a framework of constraints: Amphibian and reproductive modes. In D. Mossakowski and G. Roth (eds.), *Environmental adaptation and evolution*, pp. 87-106. G. Fischer Verlag, Stuttgart.
- West-Eberhard, M. J. 1983. Sexual selection, social competition and speciation. *Quart. Rev. Biol.* 58: 155-183.
- Wilson, B. F. and R. R. Archer. 1979. Tree design: Some biological solutions to mechanical problems. *BioScience* 29:293-298.