PHYLOGENY, ECOLOGY, AND BEHAVIOR

A Research Program in Comparative Biology

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1 Setting the Stage

Carvings and paintings on cliffs and in caves throughout the world attest to a long-standing human fascination with the relationship between organisms and their environments. This fascination has accompanied us down many cultural pathways, from the bestiaries of medieval Catholicism, through the surrealistic paintings of Rousseau, to whale songs. It has also resulted in centuries of natural history observations, the outcome of which was the accumulation of a vast, but only loosely connected, biological data base by the early nineteenth century. Darwin forged the connections with his proposal that evolution was the unifying principle in biology. His original conceptual framework included two components. First, all organisms are connected by common genealogy (Darwin 1872:346).

> The characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, all true classification being genealogical.

And, second, the form and function of organisms is closely tied to the environments in which they live (Darwin 1872:59).

> Slight modifications, which in any way favoured the individuals of any species, by better adapting them to their altered conditions, would tend to be preserved; and natural selection would have free scope for the work of improvement.

Over the past century, many specialized research programs have emerged from these two postulates. Every one of these budding disciplines initially incorporated both genealogical (phylogenetic) and environmental (adaptational) factors into their explanations of evolutionary change. However, the role of phylogeny has been progressively diminishing in some fields, most notably in ecology, ethology, and the physiological sciences, while in other fields, most notably systematics, the role of the environment has been virtually eliminated from evolutionary explanations. This, in turn, has led to the emergence of markedly different worldviews even within evolutionary biol-

ogy. Gareth Nelson summarized these perceptual differences in a discussion at a biogeography conference at the American Museum of Natural History in 1979. He told an apocryphal story of two biologists, one an ecologist and the other a systematist, who stepped into a large room together. Suspended from the ceiling by a variety of supports were thousands of balls of many different colors and sizes. All at once the supports were cut, and all the balls dropped from the ceiling, hit the floor, and began bouncing around the room. The ecologist exclaimed, "Look at the diversity!" whereupon the systematist said, "Hmm, thirty-two feet per second per second!"

The Darwinian revolution was founded on the concept that biological diversity evolved through a combination of genealogical and environmental processes. Although in theory the majority of biologists still adhere to this proposition, in practice phylogenetic and ecological studies are often conducted quite independently. Is this a problem? In order to answer this question, let us consider the following thought experiments. Suppose we were to pick, at random, any organism from a designated tide pool and a crab from anywhere in the world. If we then asked for a list of morphological, behavioral, and ecological characteristics of the unknown organism from a given environment and of the known organism (a crab) from an undetermined habitat, we would expect that more of the predictions would be correct for the crab than for the unknown tide-pool organism. In this system, we can make better predictions by reference to genealogy than to current environments. Now, consider an alternative example. Suppose we chose, at random, a finch from a Galapagos island and attempted to predict its beak morphology based upon knowledge of its feeding ecology and its phylogenetic position. In this case, we would expect ecology to be more informative than genealogy. So it appears that Darwin's original intuition was correct: evolutionary explanations require reference both to phylogeny and to local environmental conditions. The answer to the preceding question is thus, Yes, the dissociation of phylogenetic and ecological studies is an important problem because the exclusion of either perspective will weaken our overall evolutionary explanations.

This answer leads us to two new questions: Given the conceptual framework proposed by Darwin, how did this dissociation come to be? How can communication between ecology and systematics and between behavior and systematics be reestablished? In order to answer the first question we must examine the history of the two disciplines. This in itself has formed the central theme for numerous papers, books, and book chapters (see, e.g., Kingsland 1985; McIntosh 1985, 1987; Lauder 1986; Hull 1988; McLennan, Brooks, and McPhail 1988; Burghardt and Gittleman 1990), so we will present only a brief summary of the subject in this chapter. Answering the second

question requires the development of a research program that will allow us to integrate ecological, behavioral, and historical information to produce a more robust picture of evolution. We are calling this integration historical ecology, and we will dedicate the remainder of this book to delineating the conceptual, methodological, and empirical foundations of this research program.

[margin handwriting: integration of ecological, behavioral, and historical information]

The "Eclipse of History" in Ethology   (Behavior)

Ethology, as a science, was founded upon a tradition of investigating behavior within an explicitly phylogenetic framework. Darwin started the ball rolling when he compared, among other things, the behavior of two species of ants within the genus *Formica* in an attempt to trace the evolution of slave making in ants. Following this example, the "founding fathers" of ethology, Oskar Heinroth and Charles O. Whitman, proposed that there were discrete behavioral patterns which, like morphological features, could be used as indicators of common ancestry. Whitman's (1899) views mirrored Darwin's: "instincts and organs are to be studied from the common viewpoint of phyletic descent." This perspective served as the focal point for a plethora of studies in the early twentieth century. Behavioral data were examined with an eye to their phylogenetic significance for birds, including anatids (ducks and their relatives: Heinroth 1911; Herrick 1911), weaver birds (Chapin 1917), cowbirds (Friedmann 1929), and birds of paradise (Stonor 1936); and for insects and spiders, including wasps of the family Vespidae (Ducke 1913), bumblebees (Plath 1934), caddisfly larvae (Milne and Milne 1939), termites (Emerson 1938), social insects in general (Wheeler 1919), and spiders (Petrunkevitch 1926). Wheeler (1928:20) reiterated Darwin's and Whitman's perspective and reaffirmed the basis of ethological studies at the time.

> Of late there has been considerable discussion . . . as to the precise relation of biology to history . . . and what most of us older investigators have long known seems now to be acceded, namely that biology in the broad sense and including anthropology and psychology is peculiar in being both a natural science and a department of history (phylogeny).

[margin handwriting: Evol. Psych]

Comparative behavioral studies flourished under the direction of Konrad Lorenz and Niko Tinbergen during the 1940s and 1950s. Both of these ethologists repeatedly emphasized two distinct but related points: behavioral patterns are as useful as morphology in assessing phylogenetic relationship, and behavior does not evolve independently of phylogeny. Lorenz (1941) stated that "all forms of life are, in a way, phylogenetic attainments whose special objects would have to remain completely obscure without the knowledge of

their phylogenetic development," and (1958), "every time a biologist seeks to know why an organism looks and acts as it does, he must resort to the comparative method." Tinbergen (1964) outlined the comparative method:

Comparative method

> The naturalist . . . must resort to other methods. His main source of inspiration is comparison. Through comparison he notices both similarities between species and differences between them. Either of these can be due to one of two sources. *Similarity* can be due to affinity, to common descent; or it can be due to convergent evolution. It is the convergences which call his attention to functional problems. . . . The *differences* between species can be due to lack of affinity, or they can be found in closely related species. The student of survival value concentrates on the latter differences, because they must be due to recent adaptive radiation.

In other words, the phylogenetic relationships among species provide the **pattern** from which explanations of **processes** responsible for behavioral evolution within species must be derived.

Although the comparative approach to studying behavioral evolution flourished during the 1950s and 1960s, skepticism mounted about Lorenz's assertion that species-specific behavioral characters were valuable systematic characters. By the centenary of the publication of Darwin's book, two widely divergent viewpoints were held.

Behavior vs. morphology

> To assume evolutionary relationships on the basis of behavior patterns is not justifiable when such findings clearly contradict morphological considerations. The methods of morphology will therefore remain the basis for the natural system [of classification]. (Starck 1959, cited in Eibl-Eibesfeldt 1975:223)

compare. con'trend w/ Morph. vs. Molecular

> If there is a conflict between the evidence provided by morphological characters and that of behavior, the taxonomist is increasingly inclined to give greater weight to the ethological evidence. (Mayr 1958)

This difference in opinion was founded, in part, upon continuing unresolved debates among ethologists. Two questions recurred; first, how well can sequences of ancestral and derived traits be determined for attributes that left no fossil record, and, second, how well can similarities due to common ancestry (homology) be distinguished from similarities due to convergent evolution (analogy) (Boyden 1947; Lorenz 1950; Tinbergen 1951; Schneirla 1952; Michener 1953)? The question of homology was problematical because homologous characters were defined by their common origin and, at the same time, were used to reconstruct phylogenetic relationships. The inherent circularity in such a method bothered many biologists. Remane (1956) proposed a set of criteria for testing hypotheses of common origin (homology) without

a priori reference to phylogeny. These were (1) similarity of position in an organ system, (2) special quality (e.g., commonalities in fine structure or development), and (3) continuity through intermediate forms. Although authors did not agree about the universal applicability of Remane's criteria to behavior, the majority accepted that the criterion of special quality, studied at the level of muscle contractions (fixed action patterns), was the fundamental tool for establishing behavioral homologies (Baerends 1958; Remane 1961; Wickler 1961; Albrecht 1966). Initial attempts to homologize behavior in this way were admittedly vague and simplistic when compared to the more quantitative methodology of comparative morphology, but this reflected more the youth of the discipline than a fundamental flaw in the behavioral traits themselves. Time and again, phylogenies reconstructed using behavioral characters mirrored those based solely on morphology. However, in a scathing review of the ethologists' research program, Atz (1970) made only a cursory reference to these successes when he concluded,

> The number of instances in which behavior has provided valuable clues to systematic relationships has continued to grow but it should be made clear that the establishment of detailed homologies was seldom, if ever, necessary to accomplish this. . . . Functional, and especially behavioral, characters usually do not involve demonstrable homologies, but depend instead on resemblances that may be detailed and specific but nevertheless cannot be traced, except in a general way, to a common ancestor. . . . Until the time that behavior, like more and more physiological functions, can be critically associated with structure, the application of the idea of homology to behavior is operationally unsound and fraught with danger, since the history of the study of animal behavior shows that to think of behavior *as* structure has led to the most pernicious kind of oversimplification.

This review marked the end of attempts to homologize behavior, and the beginning of the "eclipse of history" in ethology.

Lorenz (1941) cautioned, "The similarity of a series of forms even if the series structure arises ever so clearly from a separation according to characters, must not be considered as establishing a series of developmental stages." In his opinion, without reference to phylogenetic relationships, the criterion of similarity was, of itself, a dangerously misleading evolutionary marker. Unfortunately, the Gordian knot of behavioral homology drove ethologists towards a new methodology based, in direct contrast to Lorenz's warning, upon arranging behavioral characters as a "plausible series of adaptational changes that could easily follow one after the other" (Alcock 1984:432). Although intuitively pleasing, this method relies heavily on subjective, a priori assumptions concerning the temporal sequence of ethological modifications

and dissociates character evolution from underlying phylogenetic relationships. This dissociation of history from behavioral evolution has had an important impact on both the nature and direction of ethological research.

The "Eclipse of History" in Ecology

Ecology is founded upon the search for an understanding of the interactions between an individual and its environment. This simple aim masks a Herculean challenge, for the term "individual" encompasses practically all biological levels, from the organism through the species to the ecosystem. The complexity of this search prompted Moore (1920), in the opening paper of the first number of *Ecology,* to call for an integration of ecology with other sciences.

> There have been three stages in the development of the biological sciences: first, a period of general work, when Darwin, Agassiz and others amassed and gave their knowledge of such natural phenomena as could be studied with the limited methods at hand; next, men specialized in different branches and gradually built up the biological sciences which we know today; and now has begun the third or synthetic stage. Since the biological field has been reconnoitred and divided into its logical parts, it becomes possible to see the interrelations and to bring these related parts more closely together. Many sciences have developed to the point where contact and cooperation with related sciences are essential to full development. Ecology is in this third stage.

Over the next thirty years, the call for integration and cooperation was answered by disciplines such as forestry and geology. Communication with systematists developed more slowly, however, and this period saw only a handful of studies exploring ecological questions within a historical framework (see, e.g., Baker 1927; Rau 1929, 1931; Parker 1930; Talbot 1934, 1945, 1948; Park 1945; Park and Frank 1948; Smith and Bragg 1949). Although numerically small, this research foreshadowed the emergence of a phylogenetically based perspective in ecology at the same time that this theme was being developed in ethology. On one side of the Atlantic, Lorenz (1941), drawing on his observations of anatid ducks, was emphasizing the importance of phylogeny to studies of behavioral evolution. On the other side of the ocean, Bragg and his co-workers were reaching a similar conclusion from their extensive studies of the ecology and natural history of toads (Bragg and Smith 1943).

> Since variations in ecological conditions (physical or biotic) markedly affect the lives of individual organisms, and through this, of species, it follows that there is a broader line between the usual

ecological emphasis upon succession of communities to the climatic or edaphic climax of a given region, on the one hand, and the taxonomic and geographic distributional emphasis of taxonomists and biogeographers on the other. The study of habits of animals, interpreted in the light of both ecology and taxonomy is, thus, an aid—indeed an absolute essential—to a complete understanding by either group of workers of the peculiar problems of either.

The next twenty-five years were characterized by two significant changes: the appearance of papers by systematists in ecological journals, echoing this sentiment of cooperation (e.g., Sabrosky 1950; Davidson 1952; Constance 1953; McMillan 1954), and a burst in the number of comparative studies (see, e.g., Pavan, Dobzhansky, and Burla 1950; Hairston 1951; Dobzhansky and da Cunha 1955; Carpenter 1956; MacArthur 1958; Kohn 1959; Cade 1963; Rand 1964; Schoener 1965, 1968; Shoener and Gorman 1968; Brown 1971; Preston 1973; Laerm 1974; Roughgarden 1974; McClure and Price 1975). The ascension of the comparative approach coincided with the appearance of the "new" evolutionary ecological perspective developed by Hutchinson and MacArthur. This research program was primarily concerned with attempting to answer the general question, Why are there so many species? and its corollary, How do these species manage to coexist? Answers to these questions had traditionally been sought within a comparative framework, an approach that was reinforced by MacArthur's (1958) statement that "ecological investigations of closely-related species then are looked upon as enumerations of the diverse ways in which the resources of a community can be partitioned." The importance of searching for evidence of competitive exclusion within a closely related group of organisms was emphasized by King (1964) in his critique of MacArthur's broken-stick model of species abundance.

As realized by Darwin (1859), the principle of competitive exclusion is most applicable to closely related sympatric species (that is, to species of high taxonomic affinity) having similar but not identical niches. This may be related to the MacArthur model since when competitive exclusion has taken place, the species of high taxonomic affinity that remain may be expected to have niches which are non-overlapping but contiguous. Hairston (in Slobodkin, 1962) suggests that tests of these species should display better fits to the MacArthur model than do tests of all species occurring in the habitat. That these predictions are valid was first indicated by the striking fits obtained by Kohn (1959, 1960) when only members of the genus *Conus* were examined. Subsequent investigations of fresh-water fishes . . . reveal that in one collection from a single locality members of the class do not fit well, but when members of the same family are considered the fit is much better.

MacArthur set the tone for ecological studies of species coexistence and the search for correlations between changes in a species' ecology and changes in the environment. However, although evolutionary ecologists were examining experimental data within a comparative framework, few researchers were incorporating phylogenetic information into their evolutionary explanations. The difference between asking a question within a historical context and incorporating historical information into the answer is a critical and, at first, counterintuitive one. Consider the following simple example. Suppose you are interested in the question of species coexistence. As MacArthur noted, the best place to look for the factors involved in species coexistence is among sympatric populations of congeners. The assumption behind this recommendation is a historical one: members of the same genus should theoretically share a number of ecological, morphological, and behavioral characters in common because they are all descended from a common ancestor. The recognition that the genealogical relationships among species may influence the outcome of an experimental investigation is the first step in any evolutionary ecological study. Having discovered an appropriate group of sympatric congeners, you set about collecting a wealth of data concerning feeding behavior, habitat preference, and breeding cycles, in order to identify the way(s) in which the species are partitioning their environment. This second step in your study is primarily nonhistorical because it requires that you make assumptions about the evolutionary *past* of species' interactions, based upon characters and interactions observed in the *present* environment. What is missing here is information about the evolutionary origin and elaboration of the characters and of the associations themselves. So, when we talk about "incorporating phylogenetic data into an evolutionary explanation," we are referring to the combination of both *the history of the species* and *the history of the traits that characterize interactions among those species*.

By the early 1970s the recognition that a collaboration between ecologists and systematists would be mutually beneficial had progressed so far that E. O. Wilson (1971) submitted a paper about the "plight of taxonomy" as a research program to an ecological journal.

> In the fashion rankings of academic biology, substantive taxonomy long ago settled to the bottom. This must not be permitted to continue. Ecologists, now beginning to savor the windfall of popularity and growing financial support, should recognize their dependence on substantive taxonomy and special responsibility to it. Most of the central problems of ecology can be solved only by reference to the details of organic diversity. Even the most cursory ecosystem analyses have to be based on sound taxonomy. . . . It is to be hoped that ecologists, in their newly acquired influence, will accept that . . . aid to their intellectual kindred, the taxonomists, is both part of their

larger responsibility to science and in their own immediate self in-
terest.

Nevertheless, the number of historically based studies began to decrease
within the rapidly burgeoning field of ecology at about the same time that the
comparative method was waning in ethology (but see, e.g., Fraser 1976;
Huey and Webster 1976; Huey and Pianka 1977; May 1977; Pitelka 1977;
Hubbell and Johnson 1978). This trend continued through the 1980s (but see,
e.g., Hixon 1980; Hairston 1981; Keen 1982; Horton and Wise 1983; King-
solver 1983; Davidson and Morton 1984; Schroder 1987; Armbruster 1988)
and, paradoxically, paralleled an increase in the number of studies concerned
with examining ecology within a specifically evolutionary context. We cannot
offer any particular explanation for this observation. Part of the answer may
stem from the perception that historical effects would confound ecological
predictions. Although "historical effects" were often considered to be a
within-species, genealogical phenomenon, there was a tendency to extrapo-
late from the genetic to the phylogenetic level. As a consequence, evolution-
ary ecologists were advised to adopt a "Goldilocks" approach (Wiens 1984)
in which the scope of their studies would not be too large for interesting
patterns to be found and not so small that similar patterns would be due
strictly to historical effects. Part of the answer may simply be that the theo-
retical foundations for ecology were well developed by the 1970s, so more
ecologists turned their attention towards a rigorous examination of the as-
sumptions underlying those theories. Although painstaking, there is no other
way to test assumptions than by a careful species-by-species examination.
And still another part of the answer may lie in an observation by Stenseth
(1984) that ecology was once the "handmaiden" of taxonomy, but became a
science on its own in the 1960s. If many ecologists felt that they had been
under the yoke of taxonomy, perhaps the break had more to do with desires
for individual identities. If so, it would be unfortunate, because many syste-
matists have felt the same way about the subordination of their discipline
within ecology. All this really tells us is that perception of subordination has
been based on mutual misapprehensions.

Whatever the reason, Ricklefs (1987) suggested that this "eclipse of his-
tory" had a profound and adverse effect on the field of community ecology.
He argued that community ecology has relied mostly on local-process theo-
ries for explanations of patterns that are strongly influenced by regional pro-
cesses. Local explanations rely on the action of competition, predation, and
disease to explain patterns of species diversity in small areas, from hectares
to square kilometers. According to this perspective, the community is main-
tained at a saturated equilibrium by biotic interactions. However, independent
lines of evidence from different communities suggest that regional diversity

plays a strong role in structuring local communities. For example, the observations that (1) there are four to five times more mangrove species in Malaysia than Costa Rica and four times more chaparral plant species in Israel than California, (2) the number of cynipine wasps on a species of California oak is strongly related to the total number of cynipines recorded from the whole range of the oak species, and (3) local species richness in Caribbean birds is strongly related to total regional bird diversity, cannot be explained solely by the assumption of local, saturated equilibria—otherwise similar states would be attained in systems exposed to similar environmental conditions.

Ricklefs concluded that "the responsiveness of the equilibrium diversity of a locality to regional processes and historical circumstances argues that coevolved interrelations among component species do not buffer community structure against externally imposed change. Accordingly, the function of a system, including its stability, does not strongly depend on its diversity." He then pointed out just how high the stakes are in our attempt to understand the origin and maintenance of biological diversity: "The threat of habitat destruction and pollution derives primarily from direct impacts rather than from loss of system stability after depauperization. However, to the extent that local communities depend on regional processes, reduction and fragmentation of habitat area will initiate a decline in both regional and local diversity to a local equilibrum, from which there can be no recovery." Ricklefs recognized the need for alternative explanations in community ecology. He also recognized the potential benefits of historical approaches, explicitly including the perspective on phylogenetic history provided by new approaches in systematics, to provide those alternatives.

Brown and Maurer (1989) reinforced this conclusion with their suggestion that general statistical regularities in ecological associations occur on much larger spatial scales than previously considered. They proposed a research field, called macroecology, in which the emphasis is on large-, rather than small-, scale studies. Like Ricklefs, they recognized that enlarging the spatial scale of evolutionary ecological studies would increase the amount of phylogenetic influence in the systems under investigation. Given the existence of these effects, then, Brown and Maurer called for ways to incorporate them into the explanatory framework of macroecology. Fortunately, this call coincides with the development of systematic methodologies that will allow us to investigate changes in behavioral and ecological characters within a phylogenetic framework.

A Revolution in Systematics

While evolutionary ecology and ethology were experiencing a surge of interest in the comparative approach, the attention of systematists was

being focussed in the opposite direction. The "new systematics," prompted by the successes of the neo-Darwinian program, emphasized studies of population variation and downplayed phylogenies. The reasons for this shift in perspective were straightforward: systematists shared the general concern that phylogenies could not be reconstructed in a noncircular manner, and evolutionary biology in general was heavily influenced by the quantum leaps occurring in population genetics. Under the influence of theoreticians such as Fisher, Haldane, Wright, and Dobzhansky, researchers sought the golden fleece of evolution in a new arena: the changes in gene frequencies within and among populations under different environmental conditions.

The "new systematics" began its reign in the 1940s. By the late 1950s and early 1960s, systematic biology experienced another revolutionary change, triggered as a reaction against a perceived lack of repeatable methodology and quantitative rigor in the discipline. Some theorists thought that these problems were inherent in any attempt to reconstruct phylogeny, and suggested evolution-free systematics (Sokal and Sneath 1963). Other believed that there could be more rigor in the evolutionary approach to systematics. These researchers, however, were faced with solving three long-standing and thorny problems: homology, levels of generalities in similarities, and characterizing useful traits. As previously discussed, Remane proposed a set of criteria for testing hypotheses of common origin (homology) without a priori reference to phylogeny. These criteria work well for establishing that some traits that appear to be "the same" are, or are not, "the same." However, certain traits that are homologous under Remane's criteria could conceivably be nonhomologous evolutionarily. This would occur, for example, if two species showing the same ancestral polymorphism experienced similar selection pressures leading to fixation of the same trait. Because the fixed trait arose more than once evolutionarily, its various manifestations among different species are not evolutionary homologues. What was needed, then, was a homology criterion that would allow workers to recognize evolutionary sequences of ancestral-to-derived traits (levels of generality) that would not be circular.

The "evolutionary homology criterion" (see Wiley 1981) that has emerged in systematics is based on the assumption that (evolutionarily) homologous traits all covary with phylogeny (since they are products of a single evolutionary history), whereas nonhomologous traits do not covary with phylogeny. To implement this criterion, systematists needed a method for reconstructing phylogeny independent of assumptions of phylogenetic history. Taxa could not be grouped according to overall similarity, because similarity embodies three different phenomena. First, there is similarity in **general homologous traits** (e.g., humans, gorillas, and elephants all have vertebrae, and vertebrae appear to have evolved only once, but the presence of vertebrae

does not help determine that humans and gorillas are more closely related to each other than either is to the elephant). Second, there is similarity due to convergent and parallel evolution (jointly termed **homoplasy**), which conflicts with phylogenetic relationships. And third, there is similarity in **special homologous traits** (e.g., birds and crocodilians have submandibular fenestrae, a trait found in no other vertebrates), which is evidence of phylogenetic relationships. Given this, two problems must be solved: distinguishing general from special traits and distinguishing homology from homoplasy. A solution to these problems was provided by the German entomologist Willi Hennig (1950, 1966).

General homol. =
symplesi-
omorphy

Special homology =
synapom.

Hennig suggested that homology should be assumed whenever possible by applying criteria such as Remane's. General homology could then be distinguished from special homology by using what is now called the "outgroup criterion" (Wiley 1981). Briefly, the outgroup criterion states that any trait found in one or more members of a study group that is also found in species outside the study group is a general trait. Hence, the presence of vertebrae in mammals is a general trait because there are nonmammals that also have vertebrae. Those traits occurring only within the study group are special similarities. The members of the study group are then clustered according to their special shared traits. If there are conflicting groupings, it means that some traits assumed to be evolutionary homologies on the basis of nonphylogenetic criteria are actually homoplasies. Because all evolutionary homologies covary, and homoplasies do not covary, the pattern of relationships supported by the largest subset of special similarities is adopted as the working hypothesis of phylogenetic relationships. As more and more traits are sampled, there will be progressively more support for a single phylogenetic pattern. Traits that are inconsistent with this pattern are interpreted, post hoc, as homoplasies. Thus, the phylogenetic systematic method works in the following way: (1) assume homology, a priori, whenever possible; (2) use outgroup comparisons to distinguish general from special homologous traits; (3) group according to shared special homologous traits; (4) in the event of conflicting evidence, choose the phylogenetic relationships supported by the largest number of traits; (5) interpret inconsistent results, post hoc, as homoplasies. So homologies, which indicate phylogenetic relationships, are determined *without* reference to a phylogeny, while homoplasies, which are inconsistent with phylogeny, are determined as such *by* reference to the phylogeny.

The advent of phylogenetic systematics marked a return to the position advocated by Darwin in 1872: "community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions and the mere putting together and separating of objects more or less alike" (346). Armed

with a noncircular method for use in formulating, testing, and refining explicit hypotheses of phylogenetic relationships by the late 1960s and early 1970s, systematists were in a position to begin contributing detailed information about phylogenetic effects on evolving systems of many kinds. And indeed, a variety of applications, derived from phylogenetic analyses using morphological data (including the micromorphological data represented by biological molecules) have been suggested (e.g., Michener 1970; Ashlock 1974; Rosen 1975; Eldredge and Cracraft 1980; Brooks 1981; Lauder 1981; Nelson and Platnick 1981; Wiley 1981; Fink 1982). By this time, however, systematists had virtually abandoned ecological and behavioral data as primary indicators of phylogenetic relationships. Their apprehensions stemmed, in part, from legitimate concerns about the dynamic nature of functional, as opposed to structural, traits. After all, verbs are intuitively more labile than nouns. These apprehensions have persisted, and a vast data base of ecological and behavioral characters remains virtually unexplored by systematists. In fact, the current state of affairs is still best summarized in a paper presented by R.D. Alexander (1962) during a symposium on the usefulness of nonmorphological data in systematic studies.

> Anyone with more than a passing curiosity about the study of animal behavior soon acquires the feeling that it has been neglected too frequently in many aspects of zoology, but especially among the systematists, who have almost a priority on the comparative attitude. . . . Behavioral attributes are . . . too often at the core of diverse problems in animal evolution to allow us to get by with the vague feeling that structure and physiology can be compared but behavior cannot—that a structural description is important information but that a behavioral description is a useless anecdote.

And so today we stand at a branching point between evolutionary ecology/ethology and systematics. The first has increasingly turned its gaze towards patterns of variation within species (microevolution), whereas the second has become preoccupied with among-species patterns (macroevolution). Strangely, this dichotomy has returned us, more than a century later, to Darwin's two theories of evolution, one emphasizing genealogy, and the other adaptation. What is strange is not that the disciplines have separated along these lines, but that they separated at all. Darwin's greatest contribution lay in his attempt to consolidate his two theories within a unified framework of "evolution," in which genealogy, or common history, explained the similarities that bound all living organisms together, and natural selection, or adaptation, explained the differences. A reunification of ecology and systematics will return us to this multidimensional view of evolution. And, as many biologists are beginning to realize, this reunification is long overdue.

The Reemergence of Macroevolution as an
Evolutionary Phenomenon

The distinction between microevolution and macroevolution was first made when Goldschmidt (1940) proposed that there were two separate evolutionary mechanisms at work. He believed that microevolution encompassed processes such as natural selection and genetic mutations. These processes operated at the population level to produce differences within species. Macroevolution, on the other hand, involved the production of new species from chromosomal mutations regardless of the effects of natural selection. Goldschmidt's ideas were opposed by the major founders of the new synthesis, or neo-Darwinism. Dobzhansky (1937), Mayr (1942), and Simpson (1944) advocated the "extrapolationist view" (Eldredge 1985) in which macroevolution was seen simply as microevolution "writ large" (see also Lande 1980b; Charlesworth, Lande, and Slatkin 1982). Mayr (1942:291) summarized this position succinctly.

> There is only a difference in degree, not one of kind, between the two phenomena. They gradually merge into each other and it is only for practical reasons that they are kept separate.

In other words, although macroevolutionary patterns may exist, their existence is due to the effects of microevolutionary processes.

The ascension of phylogenetic systematics provided biologists with an additional rigorous methodology to study both the patterns and mechanisms of evolution (Eldredge and Cracraft 1980). As a consequence, a new perspective is now emerging, based on the concept that evolution results from a variety of interacting processes, termed "forces" or "constraints," operating on different temporal and spatial scales. Evolutionary processes that occur at rates fast enough to be manifested as change within a single species lineage (**within-species** patterns) are included within the domain of **microevolution.** By contrast, processes that occur at slower rates, so that their effects are manifested in **among-species** patterns, are consigned to the realm of **macroevolution.** Microevolution and macroevolution are thus considered to be parts of a more inclusive whole represented by the hierarchical nature of biological systems (e.g., Gould 1981; Salthe 1985; Eldredge 1985; Futuyma 1986; Brooks and Wiley 1988). Since macroevolution is neither autonomous from nor reducible to microevolution, robust evolutionary explanations require data from both sources. For example, because macroevolutionary processes operate so slowly, they help define the boundaries within which microevolution takes place. That is, they can affect the ways in which and the extent to which local populations respond to selection pressures. In a complementary vein, microevolutionary processes strongly affect the building

blocks upon which macroevolutionary processes work. The emphasis in this new view is on holistic explanations in which the relative contributions of a number of processes can be assessed.

Despite this clarification of issues, Cracraft (1985b) noted that the term macroevolution is currently used in two different ways by evolutionary biologists. The **transformational** view emphasizes large-scale rules governing the origin of form, and large-scale adaptive changes. Researchers in this macroevolutionary realm search for major phenotypic differences among members of a group of species and its close relatives (see, e.g., Bock 1979; Stebbins and Ayala 1981; Alberch 1982; Ayala 1982a; Charlesworth, Lande, and Slatkin 1982; Gould 1982a,b; Maderson 1982; Levinton 1983; Stearns 1983). By contrast, the **taxic** view stresses changes in species richness within and among evolutionary groups of species. Researchers in this area are concerned with detecting influences on the rate of speciation and of extinction (see, e.g., Eldredge 1979; Eldredge and Cracraft 1980; Vrba 1980, 1984a,b; Cracraft 1982a,b; Fisher 1982; Padian 1982). These influences, in turn, may include adaptive processes (see, e.g., Mayr 1963; Jackson 1974; Vrba 1980, 1983; Jablonski 1982; Hansen 1983; Valentine and Jablonski 1983), so the distinction between the transformational and taxic approaches to macroevolution tends to blur upon close examination (Eldredge 1989). Nonetheless, Cracraft's description of these different perspectives on the evolution of biological diversity is an excellent starting point for understanding applications of phylogenetic systematics in evolutionary ecology. Over the next eight chapters, we hope to demonstrate that the "transformational" and "taxic" views of macroevolution are quite complementary.

Both the theoretical and empirical aspects of microevolution have been well developed over the last fifty years. This has allowed ecologists to make extensive use of microevolutionary principles in developing evolutionary ecology (see Collins 1986 for a review). By contrast, detailed investigations of macroevolutionary patterns were delayed until the advent of noncircular methods for reconstructing phylogenies. Prior to such investigations, evolutionary ecologists assumed that processes that could be detected *within* species, such as local demic equilibria and intraspecific competition, were also responsible for structuring (organizing) *among*-species interactions. However, the revolution in systematics was followed by a revolution in evolutionary theory, as some biologists began to believe that macroevolutionary patterns were not always microevolutionary patterns "writ large" (see Eldredge 1985 for a discussion). Gould (1981:170) summarized this new perspective.

We maintain that nature is organized hierarchically and that no smooth continuum leads across levels. We may attain a unified theory of process, but the processes work differently at different lev-

els and we cannot extrapolate from one level to encompass all events at the next. I believe, in fact, that . . . speciation by splitting . . . guarantees that macroevolution must be studied at its own level. . . . If macroevolution is, as I believe, mainly a story of the differential success of certain kinds of species and, if most species change little in the phyletic mode during the course of their existence . . . then microevolutionary change within populations is not the stuff (by extrapolation) of major transitions.

As macroevolutionary theory developed, evolutionary ecologists began to search for other processes to explain observed patterns of biological diversity, and the call was raised for the "return of history" to ecological studies. Fortunately this came at a time when some ecologists and ethologists (Ridley 1983; Clutton-Brock and Harvey 1984; Dobson 1985; Lauder 1986; McLennan, Brooks, and McPhail 1988; Pagel and Harvey 1988; Wcislo 1989) and some systematists (Brooks 1980a, 1985; Wanntorp 1983; Coddington 1988; Donoghue 1989) had already begun to bridge the gap between the disciplines. The movement to reestablish the channels of communication was based, in part, upon the (re)discovery that phylogenetic, or genealogical, constraints have played an important role in shaping the patterns of biological diversity on this planet (see Lauder 1982; Dobson 1985; Ricklefs 1987; McLennan, Brooks, and McPhail 1988; Pagel and Harvey 1988; Brown and Maurer 1989; Ferris and Ferris 1989; Gittleman and Kot 1990; Wanntorp et al. 1990). These biologists believe that persistent ancestral traits constrain the scope of the adaptively possible at every point in evolution (Brooks and Wiley 1988). Some innovations that occurred in the past have been fixed, integrated into the phenotype (the "Bauplan" of Gould and Lewontin 1979), and function as constraints on the evolution of other characters today (the "phylogenetic inertia" of Cheverud, Dow, and Leutenegger 1985; the "phylogenetic constraints" of Brooks and Wiley 1988). As a consequence, evolutionary biologists are beginning to reexamine and refine the concept of organization through constraints, one of which may be the "pull of history" (see Brooks and Wiley 1986, 1988; Endler and McLellan 1988; Gould 1989 for discussions of the various types of constraints operating in evolution).

The Emergence of Historical Ecology

By the early 1970s some researchers had begun to focus their attention on macroevolutionary patterns of diversity. Ross (1972a,b) was particularly interested in explaining these patterns for a variety of groups within the most diverse taxonomic class on this planet, the insects. Based upon his discovery that approximately only one out of every thirty speciation events in these groups was correlated with some form of ecological diversification,

Ross suggested that ecological change was consistent with, but much less frequent than, phylogenetic diversification. Furthermore, since he could not uncover any predictable patterns to explain the shifts that did occur, he proposed that ecological change constituted a biological "uncertainty principle" in evolution. Ross's interpretation of the relationship between ecological/ functional and phylogenetic diversification was certainly at odds with the traditional perspective of ecologically driven evolutionary change. Within a few years, Ross's insights were corroborated by other studies. Boucot (1975a,b, 1981, 1982, 1983) reported that the majority of ecological changes leaving some trace in the fossil record occurred out of time phase with periods of phylogenetic diversification. Like Ross, he concluded that ecological change lagged behind morphological and phylogenetic diversification, or "evolution takes place in an ecological vacuum" (Boucot 1983).

Brooks (1985) consolidated the research of authors such as Ross and Boucot, as well as the results from his own studies with parasitic organisms, into a discipline that he called **historical ecology.** Subsequent to this, we discovered a paper by Rymer (1979) in which the same term had been used to describe a research program that, today, is generally called paleoecology. This overlap highlights an important and often confusing aspect of the term "historical": it has been applied in at least two contexts. "Historical" *sensu* Rymer refers to the reconstruction of past environments, whereas "historical" *sensu* Brooks refers to the reconstruction of phylogenetic relationships. Although different, both are components of historical ecology, because phylogenetic hypotheses about changes in ancestral species are strengthened by information about those ancestors' environments.

Initially, historical ecology *sensu* Brooks (1985) was concerned with studying macroevolutionary components of ecological associations, such as host-parasite or herbivore-plant systems, or communities and biotas. In this book, we will expand the boundaries of historical ecology to include two general evolutionary processes, speciation and adaptation. We will explore the macroevolutionary effects of these processes in the production of both evolutionary groups of organisms and multispecies ecological associations.

We will ask two kinds of macroevolutionary questions about groups of organisms. First, how did a given species arise? In order to answer this, we must explore a variety of ways in which descendant species are produced from an ancestral species (speciation). Second, how did a given species acquire its repertoire of behavioral/ecological characters? This question moves us into the more familiar realm of the relationships between an organism and its environment (adaptation). In this case, however, these relationships will be examined within the context of phylogeny.

Answering both these questions will provide a data base for investigating the macroevolutionary components of biological diversity. According to the

traditional evolutionary scenario, diversity is influenced by speciation, which provides the raw materials, and adaptation, which shapes these materials to fit the environment. However, the studies by Ross (1972a,b) and Boucot (1983) indicate that ecological change may be evolutionarily conservative. If this is true, then we must ask, What is organizing biological diversity, if not adaptation? Part of the answer to this question lies in the cohesive influences of persistent ancestral traits. For example, some adaptations that originated in the past may become fixed and inherited relatively unchanged for long periods of time. These slowly evolving traits come to characterize genealogical groups of species, or clades, and function to constrain the scope of the adaptively possible at every point in the evolution of those clades (Brundin 1972; Riedl 1978; Lauder 1982; Brooks and Wiley 1988). Since the existence of persistent ancestral traits is a reflection of common ancestry, and common ancestry is a component of the speciation process, it appears that speciation may have been a more important evolutionary influence than previously thought. If this is true, then biological diversity should be structured primarily by shared ancestral characteristics (phylogenetic patterns), and secondarily by adaptive changes (functional fit to a current environment).

Having investigated speciation and adaptation processes within a group of organisms, we will turn our attention to the effects of these processes on interactions between groups. We will ask three basic questions within the context of multispecies ecological associations: How did a set of co-occurring species come to be in the same geographic area? How did co-occurring species exhibiting strong ecological interactions come to be associated? How did the traits characterizing those interactions come to be? Answering these questions will provide a data base for investigating the macroevolutionary component of biological interactions.

So, let us apply the "theory" of historical ecology to some hypothetical, biological observations. This example will center on a large, white predator (species X) living in the arctic, and the question, Why is this species white? A traditional approach to answering this question might be: (1) observation: "white" individuals are cryptic in the arctic environment; (2) hypothesis: white is selectively advantageous (i.e., at some time in the past individuals bearing white coats gained a large enough selective advantage over nonwhite individuals to promote the spread of white throughout the population/species); (3) prediction: white individuals will be "better" at acquiring either food or mates than their nonwhite counterparts; (4) research: test the predictions with a series of studies on mate choice and foraging behavior. The success of these studies requires that "white" is sufficiently variable to be quantified and compared among individuals. If coat color is a fixed trait, however, there is no way to test the hypothesis. Additionally, even if coat color does prove to be variable, studies concentrating on only one species are

investigating only one aspect of the evolution of white coats, that is, its maintenance in that species. This kind of analysis does not address the mechanisms by which a shift from the ancestral coloration to white occurred, nor does it address the question of the environmental conditions under which the trait arose and was fixed in the first place.

A historical ecological analysis would approach the problem by investigating the questions presented in table 1.1. Suppose that our investigations of the first two questions revealed (1) the ancestor of species X lived in an arctic habitat, and the speciation event producing species X and its closest relative occurred in that environment, and (2) white coat color originated in the ancestor of X. The first step in the evolution of white coat color has now been traced: white originated in an arctic environment, and its presence in species X is an ancestral legacy. Flushed with success, we turn our attention to the next problem, the potential mechanisms promoting the shift from ancestral coat color (say, brown) to white in the ancestor of X. This phase of the analysis requires that we search for correlations between white coat color and other ecological traits throughout the evolutionary history of the group of species to which X belongs. For example, one hypothesis might be that coat color in general is correlated with hunting behavior, and that white in particular is associated with hunting seals. Examining the distribution of feeding behaviors and coat color on a phylogenetic tree for this group of organisms will reveal information about the relationships between these characters

Table 1.1   Investigation of the evolutionary ecological question, Why is species X white? from a historical ecological perspective.

1. How, when, and in what environment did species X originate?
   Process: **Speciation**
   Minimum requirements for study: A phylogeny for the group including species X; geographical data.

2. When and in what environment did white arise? (i.e., is it a novel trait in species X or a legacy from its ancestor?)
   Process: **Adaptation**
   Minimum requirements for study: A phylogeny for the group including species X; paleoecological data would be useful but are not necessary for a preliminary investigation (reconstruction of ancestor's habitat).

3. Is the appearance of white correlated with a change in the interactions between the appropriate ancestor and other community members?
   Processes: **Cospeciation** and **coadaptation**
   Minimum requirements for study: Phylogenies for the group including species X and for other groups in the community; geographical, ecological, and behavioral data; paleoecological data would be useful but are not necessary for a preliminary investigation (reconstruction of ancestor's interactions).

through evolutionary time. Let us focus our attention on the ancestor of species X. There are three possible macroevolutionary patterns of the relationships between coat color and diet in this ancestor: (1) The shift to seal hunting arose before the appearance of white coloration. This indicates that brown, noncryptic individuals were capable of surviving by feeding on seals. (2) The shift to seal hunting and white coat color appeared at the same time (in the ancestor of species X). This relationship provides strong evidence that there is a causal link between color and hunting, supporting a hypothesis that white coat color conferred an adaptive advantage to its owners. This explanation could be strengthened if changes in coat color and feeding preferences covary throughout the evolutionary history of the entire group. (3) The shift to seal hunting arose after the appearance of white coloration. In this case, we are faced with the possibility that white individuals could not compete successfully with other members of the community and were forced to change their feeding habits in order to survive. So far, we have sought an explanation for the ancestral shift from brown to white coat color by examining character correlations within a clade. How can the possible influence of other community members on the evolution of this trait be investigated? We can address this problem by examining the distributions of color and feeding preferences on phylogenetic trees for other members of the community with which the ancestor of species X potentially interacted (answer to question 3). Basically, we are attempting to uncover the interactions occurring in the community at the time of the feeding shift and coat color change in that ancestor. For example, we may discover that the change in feeding preference was associated with both a change in coat color and the appearance of a new competitor in the community. This additional piece of macroevolutionary information further strengthens our adaptive hypothesis; white coat color conferred an adaptive advantage to its owners in terms of hunting ability (predator-prey interaction) and competition with other organisms (predator-predator interactions, both intra- and interspecific).

This discussion about the evolution of white coat color in the mysterious, predatory species X illustrates some of the new perspectives that will emerge from a phylogenetic (historical) comparison. Such an analysis allows us to investigate questions concerning (1) the evolutionary origin of a character and (2) the mechanisms promoting the spread of that character once it appeared in the population. This second area is of particular interest to evolutionary ecologists, because information about the associations between traits through evolutionary time, both within one group of species and among species interacting in a community, is relevant to adaptive hypotheses. Historical ecology also offers researchers a way to investigate the evolution of traits that are currently fixed in a species; in fact, the methods of phylogenetic systematics work best with such characters.

Historical ecology is primarily interested in incorporating the origins of diversity and the historical constraints on that diversity into causal evolutionary explanations in ecology and behavior. Patterns of biological diversity, in turn, are influenced by the interactions of the evolutionary processes speciation/cospeciation and adaptation/coadaptation. In the following chapters we will investigate these processes in a variety of examples ranging through plant, invertebrate, and vertebrate systems. Our choice of examples is constrained by only two considerations, the availability of explicit phylogenetic hypotheses for the study organisms and the clarity of the examples. Since historical ecology is a young discipline, such examples are limited, but every study contributes a new piece of information to the ecological puzzle. And because of its youth, historical ecology is not committed to any particular theoretical perspective, beyond the belief that evolution unifies all living organisms. So, this is truly the most exciting time in the development of any scientific discipline: the stage of discovery. This journey of discovery will lead us down many pathways and open many previously inaccessible doors, leading to a richer explanatory framework for that most important of biological processes, evolution. As Moore (1920) concluded,

> Will we be content to remain zoologists, botanists and foresters, with little understanding of one another's problems, or will we endeavor to become ecologists in the broad sense of the term? The part we will play in science depends upon our reply. . . . the future is in our own hands.