Evolutionary Biology Today

2. What do Evolutionary Biologists do?

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One of the most common questions that people get asked is "What do you do?". When I say that I am an evolutionary biologist, most people respond with "Oh, so you study fossils". My response to this is to say that I do not work with fossils, and that I am an evolutionary geneticist. This clarification typically results in the person saying "Oh, so you work with DNA." By the time I have said that I do not actually work with DNA either, the person who asked the question begins to appear somewhat confused. It seems that many people do not really have a clear idea of what evolutionary biologists today do, the kinds of questions they seek to answer, and the approaches and methodologies they use. Of course, many evolutionary biologists do work with fossils or DNA, or both, but there are also large numbers of researchers in evolution whose work does not fit into these stereotypes. In the first part of this series, we looked at the domain of evolutionary biology. In this article, we shall look at some of the sub-disciplines of evolution, embodying slightly different questions, techniques and emphases.

As we saw in the previous article, evolutionary biology in a broad sense is a very vast field because its domain is nothing more or less than life itself: in order to understand how lifeforms evolve, we must also understand how they are made and work, how they behave and how they reproduce. Even in a narrower sense, evolutionary biology is quite broad, and different people working in the field tend to fall into several loose groupings that can be described by differences in the kinds of questions they seek to address in their research. In this article, I will describe some of these groupings, delineated in a manner that is basically
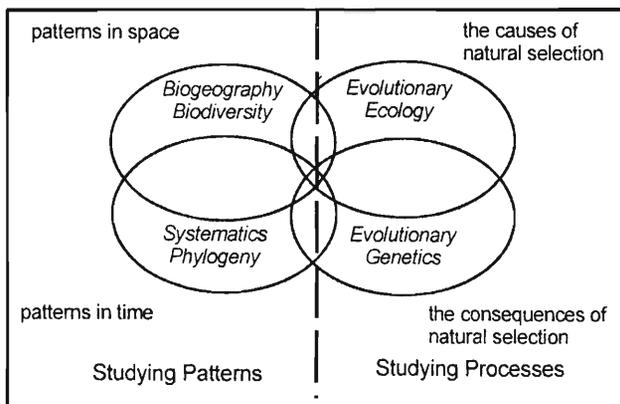
the way I like to visualize them. I stress at the outset that this is just one way of looking at the field of evolution and its sub-disciplines, and also that the boundaries between these sub-disciplines are rather blurred with the research of many scientists spilling over one or more of these boundaries.

The first major division that I like to make is between studies focussed primarily on describing and understanding patterns in the living world, and those aimed primarily at examining processes (*Figure* 1). The dotted line dividing the 'box of evolutionary biology' into two is meant to indicate that this barrier is porous. After all, patterns in the living world, whether in space or time, are generated by evolutionary processes. Clearly, then, process and pattern in evolution are intertwined, at least conceptually, as it is the process that generates the pattern, and the pattern in turn does exert feedback on the process. Yet, in terms of actual practice, researchers trying to understand patterns and those working on processes often do very different kinds of research. Within the study of patterns, we can further distinguish between research programmes primarily addressing patterns in space (the distribution of lifeforms) and those aimed at patterns in time (the history of lifeforms). Here, too, there is overlap between these two sub-disciplines, as we shall see.

Among evolutionary biologists interested in the processes underlying evolutionary change, one can broadly distinguish between evolutionary ecologists and evolutionary geneticists,

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patterns in space

Biogeography
Biodiversity

Evolutionary
Ecology

the causes of
natural selection

Systematics
Phylogeny

Evolutionary
Genetics

patterns in time

the consequences of
natural selection

Studying Patterns

Studying Processes

Figure 1. One way of envisioning the major sub-disciplines of evolutionary biology. The overlapping boundaries of the disciplines are to emphasize that these distinctions are not absolute. In The Origin of Species, Darwin himself made use of approaches and arguments that would be considered belonging to all four of the sub-disciplines depicted here, although the rudimentary knowledge of heredity in his time made it difficult for him to go into the consequences of natural selection in great detail.
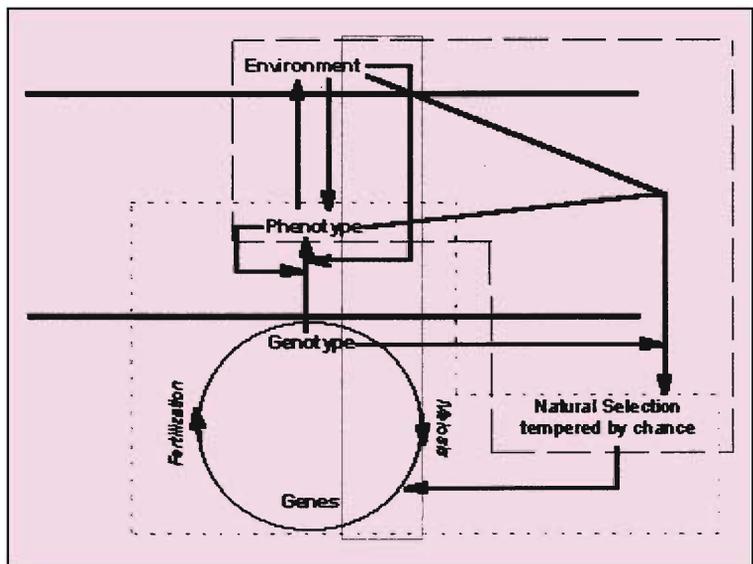
though the distinction is again a fuzzy one (*Figure* 1). In general, evolutionary ecologists tend to be more focussed on the causes of natural selection i.e. how the ecology and the life history of an organism interact to produce a force of natural selection that results in certain individuals being more successful at surviving and producing offspring than others. Or, to put it another way, evolutionary ecology is more concerned with how interaction between phenotype and environment generates differences in Darwinian fitness among different phenotypes (*Figure* 2). Evolutionary genetics is somewhat complementary to this approach and focusses more on understanding how the differences in Darwinian fitness among phenotypes ultimately result in differential transmission of genes to subsequent generations, and how these differences may eventually alter the genotypic and, therefore, the phenotypic composition of the population, resulting in adaptive evolution (*Figure* 2).

Phylogeny and Systematics

Since earliest times, humans have tried to classify living things and, especially in ancient civilizations, the detailed classification of plants and animals was often based on their significance to humans. However, there was widespread recognition that the

Figure 2. The domain of evolution. Evolutionary ecology, represented by the dashed lines, encompasses the interaction of phenotype and environment which gives rise to natural selection, because some phenotypes, by virtue of the traits they possess, are better able than others to survive and reproduce in that environment. Evolutionary genetics, represented by the area enclosed in the dotted boundary, is focussed on understanding the consequences of differences in Darwinian fitness between phenotypes. This involves understanding the genotypic differences underlying differences in phenotype, and how the differential reproductive success of phenotypes (and their underlying genotypes) will ultimately alter the genotypic (and, therefore, phenotypic) composition of the population in the next generation.

diversity of living forms was clearly discontinuous, and that distinct lifeforms (species) could be recognized, and also grouped together into hierarchical categories based on some assessment of degree of similarity. Taxonomy was quite a developed science well before the concept of evolution was widely accepted, and many workers emphasized the need to consider many different characters when assessing similarity, claiming that classification based on one or a few arbitrarily chosen characters were *artificial*, whereas a classification based on many characters would be *natural*, reflecting 'natural taxonomic categories'.

Darwin appears to have been the first to argue at length that the reason we can think of 'natural' classifications is because different species form a sort of a family tree due to descent with modification from common ancestors. In *The Origin of Species*, Darwin devoted an entire chapter to this argument, writing in the summary "In this chapter I have attempted to show that the subordination of group to group in all organisms...that the nature of the relationship by which all living and extinct beings are united by complex, radiating and circuitous lines of affinities into one grand system...all naturally follow on the view of the common parentage of those forms which are considered by naturalists as allied, together with their modification through natural selection, with its contingencies of extinction and divergence of character."

The acceptance of Darwin's ideas about adaptive evolution through natural selection changed the conceptual backdrop against which taxonomists worked, and many in the field began to argue that the purpose of a scheme of classification should be to reflect the phylogeny, or evolutionary history and interrelationships between species, rather than just providing a convenient system of nomenclature and species identification. Today, many systematists see their field as concerning not just classification and naming of organisms, but of understanding their evolutionary interrelationships and also using information on the distribution of species in time and space to make inferences about various aspects of the evolutionary process (*Box* 1).
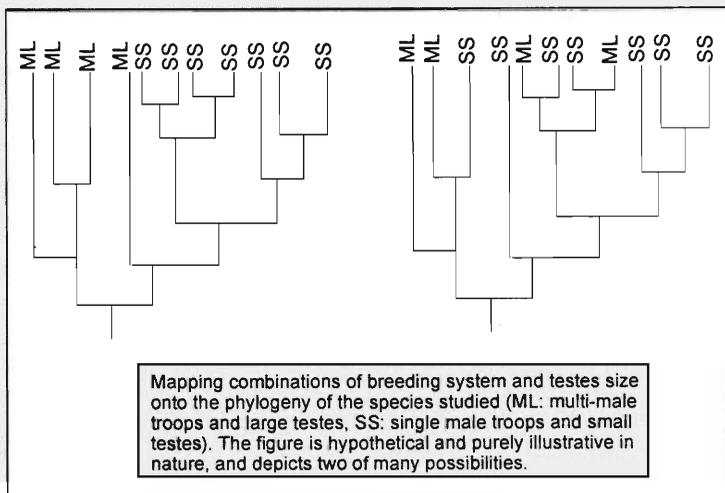
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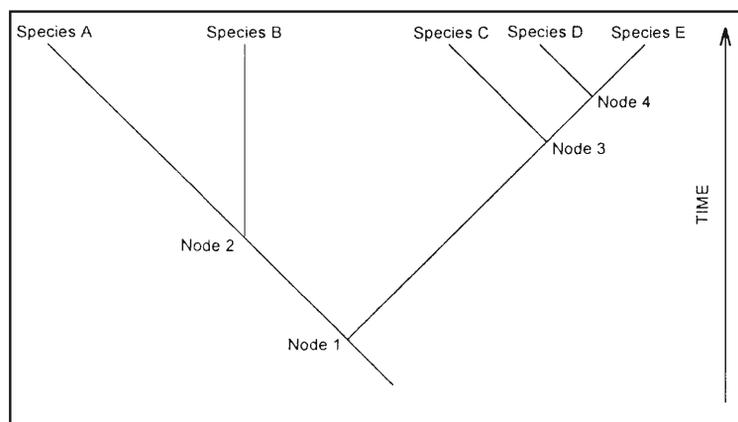
Box 1. The Comparative Method in Evolutionary Biology

The comparative method is used a lot in evolutionary biology to infer adaptation. The basic notion in applying the comparative method is to seek a correlation between two traits, or between a trait and some ecological variable, and if there is a strong correlation between the two across many species, then some inference about causation is made. For example, consider breeding systems in primates. Some species show monogamous pairing, some have single male troops where one male monopolizes matings with all the females in the troop, and yet others form multi-male troops where females may be inseminated by many males. In the latter case, we may expect relatively intense competition for fertilizing an egg among sperms from the different males that have inseminated the female. In the event of such competition, all else being equal, one could predict that males delivering more sperm in their ejaculate would have a higher chance that one among their sperm would be successful in fertilization, compared to males ejaculating a smaller number of sperms. Scientists have tried to assess whether natural selection has tended to favour males ejaculating larger numbers of sperm by looking across species of primates whether breeding system is correlated with testis size (relative to body size), such that males from species with multi-male troops have relatively larger testes than those from species with single male troops or monogamous breeding systems. The assumption here, of course, is that testis size is positively correlated with sperm count in the ejaculate, and there is some evidence supporting this assumption.

When many primate species were studied, it was indeed found that species with multi-male troops tended to have males with larger testes relative to their body size. However, to infer that this observation confirms our hypothesis that sperm competition in species with multi-male troops has led to the evolution of larger testes, we need to first rule out a possible alternative explanation, and for this we will need to know the phylogeny of the species studied. It could be that, just by chance, a particular species of primate in the past had the combination of multi-male troops and relatively large testes and all the species showing this combination today are descended from it (left hand side of figure below). If that be the case, then the data cannot be used to support our hypothesis, because there is no real 'independent' replication of the finding that multi-male troops and large testis size go together. If, on the other hand, it is seen that the combination of multi-male troops and large testes appears independently in several lineages (right hand side of figure), then we can feel more justified in claiming that the data support our hypothesis.


Mapping combinations of breeding system and testes size onto the phylogeny of the species studied (ML: multi-male troops and large testes, SS: single male troops and small testes). The figure is hypothetical and purely illustrative in nature, and depicts two of many possibilities.

The practice of phylogeny construction itself has undergone a great change in the past few decades with the development of the theory of molecular evolution, and the availability of the technology for obtaining detailed genetic information on large numbers of individuals. A phylogenetic tree of a group of species or other taxa is basically a graphic summary of the evolutionary history of that group. It tells us how closely different members of the group are related to one another, and also how long ago they shared common ancestors (*Figure* 3). Phylogenetic trees can be represented graphically in many ways that often look different. The important information conveyed in a phylogenetic tree is in the nodes, or branching points, from where two or more species (or other taxa) diverge from a common ancestor. The relative vertical distance between successive nodes on a branch should be a measure of time elapsed between the successive branchings of daughter species (taxa) from a common ancestor. The relative position of species (taxa) along the horizontal dimension does not convey any information about the similarity or relatedness of closely placed species or taxa (*Figure* 4).

In fact, the dimension of time is critical to a phylogeny. Similar tree-like diagrams (dendrograms) can in principle be made for a group of species or taxa on the basis of some measure of similarity based on many morphological or other traits. Such dendrograms are used extensively in the practice of taxonomy, and whether or not they should be considered phylogenetic trees is
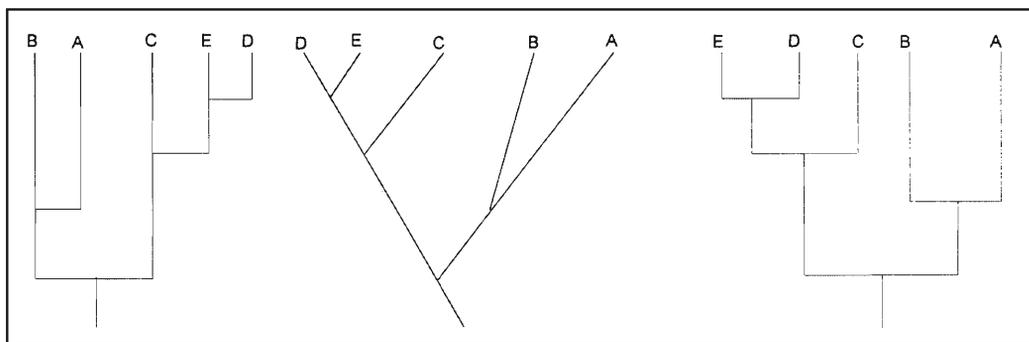
Figure 4. Alternative graphical depictions of the phylogenetic tree shown in Figure 3. It is important to note that these are all identical in the information they convey about the evolutionary relationship between these five species, even though they may look superficially different.

still a matter of some disagreement among scientists. One potential problem of evolutionary interpretation in such cases is that distances between nodes in the tree represent a measure of phenotypic similarity, not time, or even degree of relatedness (genetic similarity). Consequently, many researchers prefer genetic data over morphological data for the construction of phylogenetic trees. Whether genetic or phenotypic characters are used, there are certain criteria that a character useful for constructing a phylogeny must meet. A basic requirement is that characters used for making a phylogenetic tree should be independent, and not correlated. For example, body length and body weight will usually not be independent. The reason this is important is that very often different trees can be made that are consistent with the observed data. Statistical tests are then used to decide upon the best tree, and these tests require the characters used as input data to be independent. Another criterion is that characters used for phylogenetic tree construction should be homologous (inherited by modification from the same structure in a common ancestor). Similarity of characters reflects relatedness only if the characters are inherited from a common ancestor. In many cases, superficial similarity may be due to adaptive evolution having shaped a structure for a similar purpose in different taxa.

The independence and homology of characters can usually be tested without too much difficulty. A third criterion for characters useful for phylogenetic tree making is somewhat trickier to ensure, and this is that the characters should minimize ho-

moplasy. Homoplasy denotes noise in character data used for phylogenetic purposes. Traits may appear similar in taxa due to natural selection in similar environments, rather than close relatedness (a recent common ancestor). Conversely, some traits may differ among closely related taxa due to chance factors like random genetic drift, or because selection in different environments has caused divergence in those traits. One key here is to choose traits according to the level of taxonomic hierarchy with which one is working because it is important to choose characters which evolve neither too rapidly nor too slowly, relative to the age of the taxa for which we are constructing the tree. In the case of traits evolving too fast, differences based on different ancestry can get obliterated; if traits evolve too slowly, differences among taxa may not be seen at all.

Here we can only sketch the barest outline of the kinds of problems on which researchers in phylogeny and systematics work. It is useful to differentiate between research done to develop new methodologies for phylogeny construction and research done with the aim of collecting data to construct a phylogenetic tree for a particular group of taxa. The former research has leaned heavily on mathematical and statistical theory and, more recently, on computer science. Once we have collected data on carefully chosen characters across a number of taxa, we need to ask the question: which phylogenetic tree is most consistent with these data? Broadly, there are two types of statistical approaches used to answer this question. Parsimony based approaches seek the tree that will minimize the amount of evolutionary change required to explain the data. Maximum likelihood approaches try to find the tree which has the greatest probability of yielding the observed pattern of data under some underlying model of how the characters change. For large data sets, where the number of possible trees can get astronomically high, developing efficient algorithms to find the 'best' tree is in itself an active research area combining statistics and computer programming. Developing models for character change, especially for genetic data, is a whole branch of study called molecu-

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lar population genetics. This branch of study grew out of the work of the Japanese geneticist Motoo Kimura on how genes that are neither selected for or against evolve. This is a highly mathematical area of evolutionary research using mostly the theory of stochastic processes. Data collection for phylogenetic analyses can involve many methodologies, depending on the characters being studied which can range from gross morphology to anatomy to behaviour to DNA sequence. An increasingly used strategy is to make a phylogeny of a behavioural or morphological character and then compare it to a phylogeny of the same taxa based on genetic data (*Box* 1). This often allows interesting inferences to be drawn about the way in which that particular behaviour or morphological trait has evolved in that group of taxa. Phylogenetic analyses can also be useful in some very practical applications outside academic research (*Box* 2).

Biodiversity

Biodiversity today is a term we come across all the time in the media. Unfortunately though, the impression often conveyed by all the media coverage is that biodiversity studies are not much more than glorified nature excursions in which all one does is to routinely catalogue all the species found in a given area. Of course, studying what species there are in a given region is important, but this is just the first step in any attempt to study biodiversity. The ultimate purpose of serious research in biodiversity is not only to document patterns in the occurrence of lifeforms on Earth, but to understand the forces shaping these patterns, and to do this is no trivial task.

The geographical distribution of species was of considerable interest to Darwin, and also provided an initial impetus for him to begin thinking about the forces responsible for generating these patterns of distribution. Interest in understanding the forces shaping biodiversity waned somewhat in the early 20th century. This was largely because the development of the theoretical foundations of population genetics and population ecology was taking place at this time, and in the initial phase of this

Box 2. A Forensic Epidemiological Application of Phylogenetic Tree Construction

It may seem that construction of phylogenetic trees would not be of any interest outside the realm of academic research in evolutionary biology, but this is not so. In the 1990s, an American dentist who had tested HIV-positive was suspected of having infected a patient. As a follow up, many of his patients were tested and several were found to be HIV-positive. However, many of these patients also fell into one or another high risk category for contracting HIV infection, and it was not clear whether they had been infected by the doctor, or through some other source. To sort out the issue, scientists from the US Centers for Disease Control sequenced one of the genes of the virus (*gp120*) from a number of HIV-positive people in that city. The infected people sampled included both patients of the dentist and others. A phylogenetic tree of the sequence of the HIV *gp120* gene was then constructed.
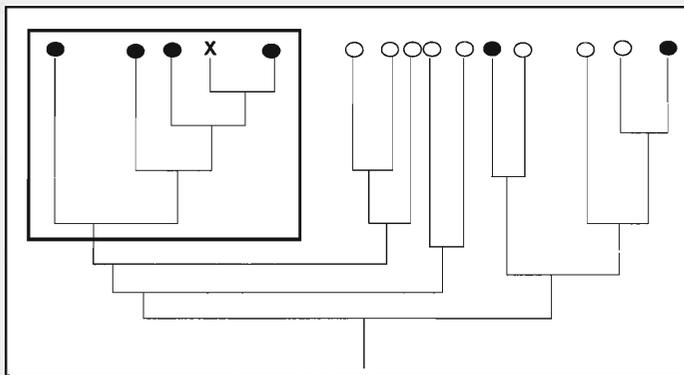
The figure shows a schematic depiction of the kind of result they obtained. In the figure, X marks the gene from the virus infecting the dentist, black circles indicate the gene from viruses from his patients, and open circles denote the gene from viruses sampled from infected individuals who were not patients of the dentist. It was clear that the *gp120* gene in the virus sampled from a majority of the dentist's patients clustered together with the gene sampled from the dentist in a distinct lineage. More importantly, HIV infected people who were not his patients did not cluster within the same part of the phylogeny as the dentist and most of his patients. The two patients on the right hand side of the figure evidently got their HIV infection from some source other than the dentist. The importance of this finding was that it confirmed the suspicion that the dentist was infecting his patients with HIV, and this confirmation then led to a number of changes being made in the way in which dentists and other doctors worked, so that chances of such transmission of HIV could be minimized in future. Similar evolutionary approaches to understanding the spread of infectious diseases have been successfully used in several countries in the past ten years.

endeavour workers like Fisher, Wright and Haldane in population genetics, and Lotka, Volterra and Nicholson in population ecology, were focussing on a detailed mathematical analysis of simple systems. With the maturation of both fields by the 1960s, a serious attempt to theoretically study the dynamics of ecologi-

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cal communities began. Particularly notable in this regard was the work of Robert MacArthur, trained as a mathematician, who turned his keen mind to community ecology. Although MacArthur died at a very young age, his theoretical work on the importance of competition and migration in shaping the dynamics of species composition on islands provided the foundation for much subsequent work aimed at understanding how the structure of ecological communities changes over time. Mac-Arthur also developed the theory of density-dependent natural selection, which recognized that different traits would be beneficial to an organism's Darwinian fitness depending on the degree of crowding an organism typically encountered. The theory of density-dependent selection represented the first step towards a merger of population genetics and population ecology which had till then developed largely separate from each other. Despite his very brief career, many ecologists feel that MacArthur was probably one of the most influential ecologists of the 20th century.

Once again, we do not have the luxury of a detailed discussion of community ecology and biodiversity studies here. I would just like to point out that, as in the case of phylogeny and systematics, research problems and researchers in this field too are of diverse kinds. Even the quantification of biodiversity raises interesting questions, and many statistically minded workers have applied their ingenuity to devise meaningful estimates of different aspects of biodiversity. The study of community structure and dynamics brings together naturalists carrying out surveys and manipulative experiments in the wild, experimentalists testing theories in carefully controlled microcosms in the laboratory or greenhouse, and theoreticians trying to understand how various ecological factors interact to affect the growth and composition of communities, a problem in complex system non-linear dynamics.

Evolutionary Ecology and Evolutionary Genetics

I will turn briefly now to the two broad areas of evolutionary

biology where the emphasis is on understanding the evolutionary process. Both the sub-disciplines, evolutionary ecology and evolutionary genetics, warrant articles on their own, in which we will look at examples of the kinds of studies that are done by practitioners of these fields in some detail. As mentioned before, the focus in evolutionary ecology studies tends to be on the fitness consequences of certain phenotypic attributes, whereas in evolutionary genetics the focus is on the evolutionary consequences of the differential fitness of phenotypes. Very often, the first problems are suggested by some application of the comparative method. For example, it has been observed for a long time that animals inhabiting colder regions tend to be larger than similar species, or populations of the same species, inhabiting warmer climates. Theoretical arguments can be made about why larger body size would be helpful in a cold climate because in a larger animal, the ratio of surface area to volume is likely to be less than in a smaller animal. Consequently, conservation of heat is likely to be easier for a larger animal, and this should help it survive better in a colder climate, resulting in higher fitness. An evolutionary ecologist would most likely follow up this reasoning by subjecting animals of different size to different temperatures and asking whether, in fact, larger animals had higher survival at colder temperatures and vice versa. An evolutionary geneticist would probably like to go a step further and say "Okay, maybe larger body size results in greater fitness at low temperatures, but since we know very little about the genetics of body size, we should still ask whether larger body size will in fact evolve in organisms living at low temperatures for many generations". He or she would then go ahead and try to do a long-term experiment in which some populations of the species were maintained for many generations at low temperatures, and then compared with those maintained at higher temperatures, to see whether larger body size actually evolved in the low temperature populations. In both these sub-disciplines, too, actual research consists of a blend of theory, experiment and observation.

Suggested Reading

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Evolutionary biology and its individual sub-disciplines are syncretic sciences in which theory, observation and experiment blend far more equitably than in many other fields in biology. Scientists from diverse backgrounds, ranging from engineering to zoology, have contributed to our understanding of the evolutionary process and its consequences.

Conclusion

In this second part of the series, I have tried to give a brief overview of the major sub-disciplines of the field of evolutionary biology. Some of these – evolutionary ecology and evolutionary genetics – will be dealt with in greater detail in subsequent parts. That is not to imply that these fields are more important than others; I will discuss them in more detail because those are the fields I happen to be more familiar with through direct experience. Another aspect that I have tried to stress here is that evolutionary biology and its individual sub-disciplines are syncretic sciences in which theory, observation and experiment blend far more equitably than in many other fields in biology. Although individual scientists may focus in their research on a particular organism and a small set of traits, they cannot afford to lose sight of the broader conceptual framework of evolution. In India, evolutionary biology as a research field is rather under represented. Yet, although few Indian scientists do research in evolution, their contributions to the enhancement of our knowledge in this field has been notable. The Suggested Reading accompanying this article have been chosen to give you a sampling of some of the work done by Indian evolutionary biologists, and I have referenced articles published in Indian journals in the hope that they will be relatively accessible to interested readers. Worldwide, scientists from diverse backgrounds, ranging from engineering to zoology, have contributed to our understanding of the evolutionary process and its consequences. Similarly, questions in evolutionary biology have often led to the development of new areas in other fields of study such as mathematics, statistics and computer science. In our country, unfortunately, evolution is taught largely as a historical footnote to classical biology courses, and I hope that these articles on evolution will appeal to students from disciplines other than biology, and help convince them that there is something for everyone in this very fascinating and inter-disciplinary study of the dynamics of life.

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