An Introduction to Evolutionary Genetics

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CONTEMPORARY BIOLOGY

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To Pat
whose unfailing encouragement makes it all worthwhile

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Preface

The theory of evolution by natural selection was proposed by Darwin and Wallace in the middle of the 19th Century, long before the rediscovery of Mendel's Laws. This book attempts to describe how the theory has itself evolved and changed in the century from its inception to the present day.

Contemporary evolutionary genetics is a complex science that combines a sophisticated theoretical framework with both a strong laboratory component and detailed field observations. I have endeavoured to review the subject at a fairly elementary level, drawing information from all three branches to give a balanced view of the basic principles. The book has evolved from courses that I have taught at Nottingham over the last seven years and reflects my own biases and interests, as well as those of the undergraduates that I have taught.

It makes no attempt to cover fields that are already represented by books in this series. Thus, the reader will find little or nothing on basic genetics, chromosome structure and evolution, or the evolutionary aspects of developmental biology.

During the time that I have been preparing this book, I have received a great deal of help from many people. In particular, I thank Professor Bryan Clarke, who read most of the manuscript, and Professor Ernest Barrington, who was noble enough to read it all. Drs. Tom Day and Jeremy Greenwood, and my graduate students Eric Verspoor and David Whitehouse, helped more than they realise by discussion and criticism of many of the topics. In addition, the undergraduates helped by their interest and disinterest, understanding and confusion. Nothing clarifies one's ideas better than having to

explain them to others. It is also a pleasure to express my thanks to Petra Gendle who typed the various drafts, and skilfully produced an ordered manuscript from my almost illegible chaos. And finally, to my wife, whose constant encouragement helped me more than I can say.

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Evolution by Natural Selection

DARWINISM

It seems almost traditional to begin a book like this with the statement that the theory of evolution by natural selection is the greatest unifying theory in biology. Nevertheless, it remains true that this one concept draws together a vast range of otherwise separate studies of the variation and distribution of living and extinct organisms. Systematics and taxonomy are only given real meaning and direction when coupled with the idea that species evolve and diverge. Similarly, comparative anatomy, physiology and embryology provide little other than academic exercises unless the interrelationships of the phenomena are made apparent by an understanding of the evolutionary process.

The importance of this theory to modern biology makes it necessary to delve at once into the past, to discover why and how Charles Darwin[64] appreciated that evolutionary change takes place through the action of natural selection imposed by the environment. For Darwin did not invent evolution. His greatest contribution to science was to suggest, and demonstrate to the best of his ability, a method by which it could, and, as we now believe, probably did, take place.

In the middle of the last century, the collecting of biological specimens from all round the world had revealed that a vast number of species of animals and plants exist upon the earth. Biologists had described and catalogued them. It had become evident from their studies that species could be arranged into groups on the basis of similarities and differences in their anatomy. Linnaeus had used this as the basis for his nomenclature, and people were now beginning to think that it reflected true relatedness. But why should this be so, and how could such systems of relationship have arisen?

Studies in geology were in the same early descriptive stage as biology. Nevertheless, they were revealing that species might not be permanent entities. There was evidence that forms present in the fossil record were lacking from contemporary faunas. Darwin had observed this for himself when he studied the fossilized remains of giant armadillo-like creatures in South America, which were quite unknown to the field biologists of the day. Conversely, it was beginning to appear likely that some species present in the fauna of the nineteenth century were absent from the fossil remains being uncovered all round the world. The appearance and disappearance of fossil forms, the geological evidence of extinction, likewise required an explanation.

The key was furnished when Darwin's voyage around the world stopped briefly in the Galapagos Archipelago,[65] five hundred miles into the Pacific Ocean off the coast of Ecuador. Here lay a mass of islands varying in size, close to the equator and, sitting in the cold waters of the Humboldt current, well isolated from continental South America. Darwin spent some time among these islands, observing and collecting the curious finches which now bear his name, and also the remarkable giant tortoises.

These two groups of animals were very interesting to him. The finches were clearly similar to one another in many of their morphological characters. For birds of their size, the wings and tail were short, and the feet and legs were rather large. Most of the forms had a plumage which was very similar in colour and pattern. Furthermore, the flight and general behaviour of the different forms had many resemblances. Despite these similarities, the variation in the size and shape of their beaks, and the differences in body size, were sufficient to produce a variety of forms of finch which appeared to be quite distinct from one another. These forms could be regarded as separate species, each being well adapted to its particular role in the Galapagos fauna.

Figure 1.1 shows examples of the various finches to be found on the single island of Santa Cruz. There are three species of seed eaters, with bills of different sizes, which spend much of their time feeding upon the ground.[165] There are arboreal seed eaters with more pointed bills, and species with shorter softer bills which feed upon buds or insects in the trees. One form is so extreme as to be almost identical with the old world leaf warbler (*Phylloscopus*) in size and shape, even flicking its wings in the same nervous manner. Perhaps most remarkable of all is the woodpecker finch which spends much of its time on

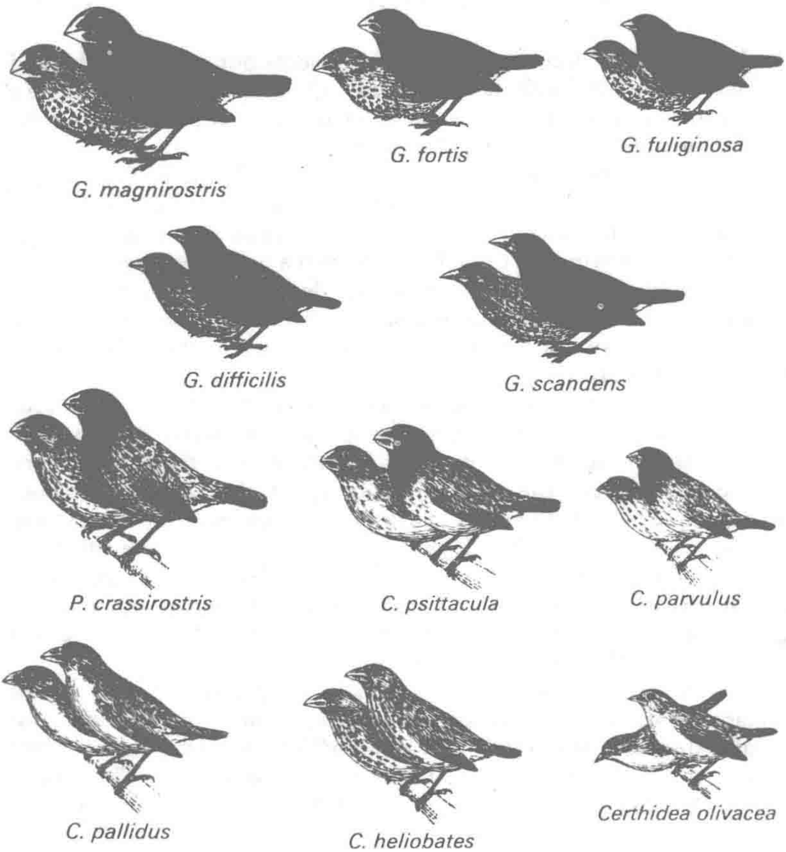

Fig. 1.1 The species of Darwin's Finches found upon the Island of Santa Cruz in the Galapagos Archipelago.
Top line The three species of ground feeding seed-eaters. Separated from one another by the size of their bills and the size of the seeds upon which they feed.
Second line *G. difficilis* is now almost certainly extinct. It lived in the humid zone and probably fed upon seeds in the trees. Separated by habitat zone from *G. scandens* which is also an arboreal seed-eater, but from the transitional and arid zones.
Third line *Platyspiza crassirostris* is distinct from all the rest since it feeds upon buds and leaves. *C. psittacula* and *C. parvulus* are both arboreal insectivores separated from one another by bill size and consequently, prey species.
Bottom line Three highly specialized forms. *Cactospiza pallidus*, the woodpecker finch, eats insects from the trunks and branches of trees. *C. heliobates* is exclusively found in the mangrove swamps. *Certhidea olivacea*, the warbler finch, feeds upon small insects collected from the foliage of trees and shrubs.
Thus all these species are distinguished on the combination of habitat and food resources. From Lack.[165]

the branches and tree trunks, picking insects out of the cracks and crevices in the bark with its rather long bill. This species will utilize a cactus spine as a tool to help extraction when the prey is too deep to be reached in a more conventional manner.

Bearing in mind the many anatomical resemblances such as wings, tails and feet, in addition to the internal features and feather number and distribution which are less visible to casual inspection, it was apparent to Darwin that these birds formed a homogeneous group. It seemed possible to him that they had descended from a common ancestor. The differences in anatomy between the species could be explained as adaptation to the particular niches in the environment which they occupied.

He found the tortoises equally remarkable. Giant tortoises occur nowhere in South America apart from the Galapagos Archipelago. Each island population is a distinct variety, and there were even differences between the populations living on the various volcanoes on one single island. In fact, Darwin was very impressed to learn from the governor of the Archipelago that it was possible to identify quite conclusively the island from which a particular tortoise originated. Again, the island forms were clearly closely related to one another, although slight differences in anatomy were to be seen which might or might not be important adaptations to survival.

A third observation which he made during his studies of the Galapagos Islands concerned variations in the flora. Some of his results are summarised in Table 1.1, which lists the number of plant species that he knew to occur on four of the large islands. The species are categorized either as Galapagos natives, or those known to occur

Table 1.1 The number of species of plants reported from four islands of the Galapagos Archipelago by Charles Darwin.

Island	Total number of species	No. of species found in other parts of the world	No. of species confined to the Galapagos Archipelago	No. confined to the one island	No. confined to Galapagos Islands but found on more than one island
James	71	33	38	30	8
Albemarle	46	18	26	22	4
Chatham	32	16	16	12	4
Charles	68	39*	29	21	8

* Or 29 if those plants which have probably been imported into the island by man are excluded.

in other parts of the world. Excluding ten species from Charles Island that he considered to have been introduced by man, Darwin estimated that over half occurred nowhere else in the world and were thus endemic to the archipelago. Furthermore, the majority of these species were in fact endemic to one single island within the group.

Present-day systematics has resulted in great modification and revision of the interrelationships of these plants, but the fact remains that the islands of the Galapagos exhibit an unusually high degree of endemism. Again, there are close similarities between the plants of several islands, and yet they show differences between the islands that are sometimes substantial.

The situation in Galapagos convinced Darwin that evolution is a major process in biology. He appreciated clearly that when a population occupied a new niche it frequently evolved in a different direction to other similar populations. Thus, the tortoises and the finches had reached the islands at some time in the past, and had evolved in a variety of directions to give the various forms present today. Many of the finch species are now found on several islands, but the tortoises and many species of plants only occur on the island where they must have originated.

Darwin's particular genius was that he was able to draw together his field observations with pertinent evidence from a variety of other sources, and to solve the conundrum of evolutionary change. There are three pieces of crucial evidence that were vital to his thesis, and we will consider them in turn.

The evidence from breeding studies

It was well-known that offspring tend to resemble their parents more closely than other members of the species. The phenomenon was not understood, but it was established as an observational fact. At this time, the laws of heredity were still quite obscure, and people tended to believe that offspring were usually the result of a blending or mixing of the characteristics of the two parents.

But even if the mechanism was not fully, or even partly, understood, the fact of parent-offspring resemblance was used, and had been used for generations, by agriculturalists and plant or animal breeders. Consciously, or unconsciously, they had been choosing their best individuals and breeding from them, while discarding the less desirable forms. This had the long-term result of modifying and improving the strain, gradually changing its appearance towards the desired end. Darwin himself had performed selective breeding experiments with pigeons, and had successfully produced modification in the appearance of some of his stocks.

The problems of extinction

Darwin believed the observation that species often became extinct to be particularly relevant. The reasons why extinction takes place need not always be the same. If the environment should change and become unsuitable, a species might fail to survive; the implication being that it was unable to adapt to the changed conditions. Thus, Newell[204] has suggested that many species of marine invertebrates became extinct during the Devonian and Permian eras due to the reduction of the area of the seas and the appearance of the major continental land masses.

Alternatively, one species could become extinct as the direct, or indirect, result of the superior performance of another. The red squirrel (*Sciurus vulgaris*) is principally an inhabitant of coniferous forest and consequently many of the woodland areas of Britain are suboptimal habitats. When the grey squirrel (*S. carolinensis*) was introduced from North America, it spread very rapidly, and there was a correlated decline in red squirrel numbers, until the latter is now very much restricted in its range. This is good circumstantial evidence that the decline of the red squirrel was caused directly or indirectly by the presence of its congener.

Intraspecific competition

It is apparent from reading Darwin's books that he was greatly influenced by the writings of Malthus, and particularly by an essay which discussed the subject of population growth. Malthus himself was primarily concerned with the social problems of man in an urban environment following the industrial revolution. He appreciated that, without adequate controls, a population would increase rapidly and geometrically. In theory, if an average pair of individuals leave four offspring, then the population will double in size every generation. It will increase over a million fold in less than 25 generations. Such geometrical growth does not usually occur, although the increase in natural populations is sometimes remarkable.

For example, in 1938, two male and six female ring-necked pheasants (*Phasianus colchicus*) were released on Protection Island in the Puget Sound, northwestern U.S.A. Six years later, the population size was estimated at 1898 individuals by Einarsen.[85–6] This means that the population had increased over 200-fold, and the island is too isolated for immigration to be involved. The increase is due to the reproductive capacity of the birds themselves, and Lack[166] reports that the prime factor is a high survival of young birds. Presumably the density was so low that mortality due to intraspecific effects was quite unimportant, and the absence of competition allowed almost maximum survival and consequently a very rapid population growth. Unfortunately, the island was occupied by the military in 1942, and the population of pheasants crashed (into the pot!). The subsequent history is not available. In other species which have undergone rapid growth, the population size stabilized out at an upper limit, and remained reasonably constant at this level. Davidson[66] reports on the number of sheep in Tasmania between 1830 and 1925. The population rose from 200 000 in 1820 to 2 million in 1850. It remained at this level for the next 70 years. It could be argued that this is not a particularly impressive example since it is subject to human control, but it could also be argued that man is exerting a level of predation which is maintaining the sheep population at or about the 2 million mark.

EVOLUTION BY NATURAL SELECTION

Populations introduced into a reasonably stable environment do not usually increase geometrically for more than a few generations. Eventually they level out at some point, perhaps fluctuating somewhat from generation to generation. Unless the reproductive strategy of the species changes, such a levelling out of the population curve implies that mortality must increase. A higher proportion of the population fails to survive to maturity in a stable situation, than in one where numbers are increasing.

Darwin believed that these ideas of Malthus were of fundamental importance in evolution. He suggested that mortality (which regulated population size) took place in such a way that the less well adapted would be the victims. This does not necessarily imply that the physically weak die, rather that those individuals which utilize the general biological environment most efficiently will be the survivors. Darwin accounted for evolutionary change through this system. Just as a breeder chooses those individuals closest to his desired optimum, and discards the rest, so the natural environment improves the performance of a species by eliminating the less effective. Individuals possessing particular adaptations will survive better, and by virtue of the heritable nature of these adaptations, they will transmit them to their offspring. Gradually, the adaptations will spread and improve, so that the species will become better suited to the environment which it inhabits.

This is the fundamental principle of evolution by natural selection, and deserves repetition. A population produces an excess of offspring and mortality occurs to reduce the numbers to a level which the environment can support. There is inherited variation for all those characters which affect the probability of survival in each individual. Those individuals that are least well adapted to the environment perish, and the survivors pass on to the next generation the potentiality of producing the very characters which allowed their survival. Thus, the nature of the population changes as a result of this natural selection: the population evolves towards a new level of adaptedness to the environment.

Let us consider this theory in relation to the finches of the Galapagos Islands. A flock of ancestral birds arrived on the islands from South America in the distant past, and found them ornithologically barren. The flock presumably settled on one island, and then indulged in the exponential growth demonstrated by Einarsen's pheasants. When that island became fully populated, and mortality increased, adjacent islands were perhaps colonized one after another until the entire Archipelago was occupied. Gradually, the island populations were evolving under natural selection, accumulating differences which improved their success on their natal island, until they reached the level of full species. Secondary recolonization of the islands from which they came could then give rise to the complex finch fauna, which was apparent to Darwin and still exists today.

There are gaps in this story, however, which classical Darwinism cannot fill. For example, how does speciation actually occur? Is it anatomical, behavioural, or ecological? What is it that delimits one species from another? Darwin[64] himself dealt with the problem by suggesting that species was a term: 'arbitrarily given for the sake of convenience to a set of individuals closely resembling one another' and that the term 'does not essentially differ from the term variety which is given to less distinct and more fluctuating forms.'

However, Darwin is not really correct here. A species is perhaps the only taxon in systematic classification which is not arbitrary. It is allowable of a much more precise definition, either genetically as 'the largest and most inclusive reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool',[76] or somewhat more biologically as 'groups of actually or potentially inbreeding natural populations which are reproductively isolated from other such groups.'[183] The important facts are that reproductive isolation exists between species, and that the act of speciation consists in its barest essentials of the establishing of such isolation.

Despite the title of his major work being 'On the Origin of Species', Charles Darwin did not actually discuss this to any great extent; he was merely concerned with establishing the fact of evolution and his thesis that it took place through the action of natural selection. Because of his loose definition of the status of a species, he did not have a problem in accounting for its origin. It is merely a grade of difference between groups of organisms that arises by virtue of natural selection acting upon the variation present in an earlier series of populations. However, we now regard a species as something more precise, and will return to the phenomenon of speciation later in this book.

THE CONTRIBUTION OF ALFRED RUSSELL WALLACE

The name of Charles Darwin must always be associated with that of Alfred Russell Wallace in discussion of the theory of evolution by natural selection, for both independently derived the theory during the mid-nineteenth century. Wallace was a very different man to Darwin, being less well educated, and a professional collector rather than a gentleman scientist. Sheppard[239] points out that the two men shared the attributes of being field naturalists of great experience and ability, with a lack of formal instruction in biology. This lack of training enabled them to view the subject with an eye unjaundiced by the dogma of the age.

The remarkable adaptations of organisms to their environment was as apparent to Wallace[264] as it was to Darwin, and the former similarly appreciated that a species produced far more offspring in a generation than the environment could support. He believed that there would be tremendous competition for food in most natural populations, and that its availability would be the principal factor controlling their size. While this is undoubtedly true in some situations, other factors can be equally important, and can be selective agents under alternative circumstances.

Evidence in support of the relevance of food supply to population dynamics has been provided by Lack,[166] with a particularly impressive result concerning the survival of nesting swifts in an Oxfordshire colony. Lack demonstrated that mortality varies considerably from year to year, and Table 1.2 shows that it is greatest in seasons when the weather is poor. He suggested that this is related to the availability of aerial insects upon which adult swifts feed their young. In summers when the weather is fine, there are plenty of insects and so the nestlings get sufficient food. In poor seasons, insect food is less readily available, and mortality is higher.

The climatic situation shows an interaction with clutch size, however, which is both interesting and instructive. Swifts usually lay either two or three eggs in a clutch. As can be seen from Table 1.2, when the breeding season coincides with fine weather and a plentiful food supply, an average of 2.3 young survive from nests containing

Table 1.2 The survival of nestling Swifts (*Apus apus*) in different years, related to the amount of sunshine, and hence to the availability of aerial insects upon which adults feed their young. From Lack.[166]

	Brood size	Number of young hatching	Proportion surviving to flying stage	Number of young raised per brood
1946 to 1948 sunshine well below average	2	48	50%	1·0
	3	36	31%	0·9
1949 to 1952 sunshine average or above average	2	156	95%	1·9
	3	60	75%	2·3

three eggs, but only 1.9 from nests with two. In poor seasons, the picture is slightly different: only 0.9 young survive from three-egg clutches, while 1.0 survive from those with two eggs. Here is an example of selection pressure imposed by food supply. In a good season, parents have no difficulty in rearing three youngsters, and leave more offspring than their two-egg neighbours. When the climatic conditions are more severe, a pair of swifts can collect enough food for two nestlings, but insufficient for three, and the whole brood starves. Consequently, more young survive from clutches of two in these years, and selection operates against parents who produce large clutches.

Food supply is not always as important as this. The possession of a territory is vital for many species of temperate song birds to be able to breed successfully, but there is no great evidence that territories are smaller in seasons when food is particularly abundant. Consequently, the densities of populations are not directly limited by food supply, although if food is locally superabundant, the survival of the nestlings may be enhanced. Wallace oversimplified the situation when he suggested that competition for food was paramount, but 100 years later, the relative importance of territory, predation, parasitism and available food supply is still a matter for considerable dispute (for a recent review, see Ricklefs).[227]

LAMARCK AND ACQUIRED CHARACTERS

The *sine qua non* of Darwin and Wallace's ideas on evolution by natural selection is the presence of inherited variation within a population. Unless a population is variable, there is nothing to select.