

Part four

Evolution and Diversity

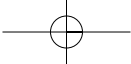
Darwin closed *The Origin of Species* with the following words:

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Part 4 of this book is about how the theory of evolution can be used to understand the diversity of life or, in Darwin's words, the "endless forms most beautiful." The units in which biologists measure the endless forms are species. We begin this set of chapters by looking at what biological species are, and also at diversity within a species. In evolutionary biology, species can be understood as gene pools — sets of interbreeding organisms — and these are important units because, in the theory of population genetics, natural selection adjusts the frequency of genes in gene pools.

The millions of species now inhabiting this planet have, as Darwin said, evolved from a common ancestor, and the multiplication in the number of species has been generated as single species have split into two. Speciation (Chapter 14) has probably often occurred when two populations have evolved independently, and accumulated incompatible genetic differences. Much is understood about this process, but we also look at some other, less well understood, ways in which new species may arise.

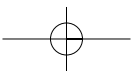
Chapter 15 describes how the phylogenetic relations of species, and higher taxonomic groups, can be reconstructed. The history of species cannot be simply observed, and



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phylogenetic relations have to be reconstructed from clues in the molecules, chromosomes, and morphology of modern species (and in the morphology alone of fossils). Phylogenetic reconstruction is a crucial part of modern taxonomy, which we look at in Chapter 16. Arguably, phylogeny provides a better principle for biological classification than any alternatives. In order to classify species, therefore, we need to know their phylogenetic relations and Chapter 16 logically follows Chapter 15.

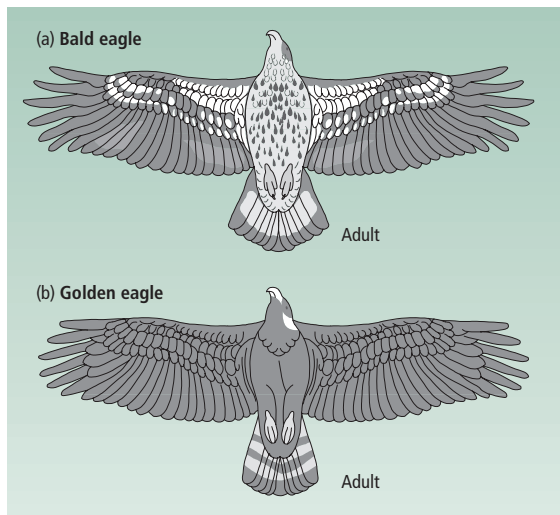
Finally, the theory of speciation, as well as classification and phylogenetic reconstruction are all needed in evolutionary biogeography (Chapter 17) — the use of evolutionary theory to understand the geographic distribution of species.



13 Species Concepts and Intraspecific Variation

Evolutionary theorists have suggested a number of reasons why biological species exist, and there has been a controversy about which of the reasons is most important. This chapter is about species concepts, and the controversy among them. We begin by seeing how species are recognized in practice, and then move on to the theoretical ideas. We take, in order, phenetic, reproductive (biological and recognition), and ecological concepts, which all aim to define species at a point in time. We concentrate on two properties of each species concept: (i) whether it theoretically identifies natural units; and (ii) whether it explains the existence of the discrete phenetic clusters we recognize as species. While looking at the biological species concept, which defines species by interbreeding, we also consider the topic of isolating mechanisms that prevent interbreeding between species. We examine some test cases from asexual organisms and from genetic and phenetic patterns in space. We then turn to cladistic and evolutionary species concepts that can supplement the non-temporal concepts and define species through time. We finish by considering the philosophical question of whether species are real categories in nature, or nominal ones.

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**Figure 13.1**

(a) Adult bald eagle (*Haliaeetus leucocephalus*) and (b) adult golden eagle (*Aquila chrysaetos*), seen from underneath. The species can be distinguished by their pattern of white coloration.

13.1 In practice species are recognized and defined by phenetic characters

Species are formally defined and practically recognized by phenetic characters

Biologists almost universally agree that the species is a fundamental natural unit. When biologists report their research, they identify their subject matter at the species level and communicate it by a Linnaean binomial such as *Haliaeetus leucocephalus* (bald eagle) or *Drosophila melanogaster* (fruitfly). However, biologists have not been able to agree on exactly how species should be defined in the abstract. The controversy is theoretical, not practical. No one doubts how particular species are defined in practice. Taxonomists practically define species by means of morphological or phenetic characters.¹ If one group of organisms consistently differs from other organisms, it will be defined as a separate species. The formal definition of the species will be in terms of characters that can be used to recognize members of that species. The taxonomist who describes the species will have examined specimens of it and of related species, looking for characters that are present in specimens of the species to be described, and absent from other closely related species. These are the characters used to define the species.

Almost any phenetic character may end up being useful in the practical recognition of species. Figure 13.1 for example shows the adults of the bald eagle (*Haliaeetus leucocephalus*) and the golden eagle (*Aquila chrysaetos*), seen from below. A bird guide will

¹ Phenetic characters are all the observable, or measurable, characters of an organism, including microscopic and physiological characters that may be hard work in practice to observe or measure. Morphological characters are characters of the shape or observable form of the whole organism or a large part of it. Behavioral and physiological characters are part of the phenetic description of an organism, but not part of its morphology. However, taxonomic descriptions are usually made from dead specimens in a museum, and the phenetic characters that are specified in taxonomic descriptions are usually morphological characters. The words “phenetic” and “morphological” are therefore practically almost interchangeable here. Also, the word “phenotypic” could be used instead of “phenetic.”



Box 13.1

Description and Diagnosis in Formal Taxonomy

The point of the example of the two eagle species is intended merely to demonstrate that species are defined in practice by observable phenetic characters. We should also notice a terminological formality, distinguishing between a formal *description* of a species and a *diagnosis*. The formal definition is the description of the species — in terms of phenetic characters — that a taxonomist originally supplied when naming the species. Certain rules exist about the naming of new species, and the characters specified in the formal definition are the “defining” characters of the species in a strictly formal sense.

The formally defining characters of a species may be difficult to observe in practice. They might, for instance, be some fine details of the creature’s genitalia, which can be recognized only by an expert using a microscope. Taxonomists do not on purpose pick obscure characters to put in their definitions, but if the only distinct characters that the species’ first taxonomist noticed were obscure ones then they will provide its formal definition. If the formally defining characters are inconvenient to observe, subsequent taxonomists will try to find other characters that are more easily

observable. These useful characters, if they are not in the formal description, provide what is called a “diagnosis.” A diagnosis does not have the legalistic power of a description to determine which names are attached to which specimens, but it is more useful in the day to day practical taxonomic task of recognizing which species specimens belong to. As research progresses, better characters (i.e., more characteristic of the species and more easily recognized) may be found than those in the first formal description. The formal definition then loses its practical interest, and the characters given in a work like Peterson’s *Birds* are more likely to be diagnostic than formally defining.

When an evolutionary biologist discusses the definition of species, the formal distinction between description and diagnosis is beside the point. All that matters is that phenetic characters are used to recognize species, as in the eagles. The distinction is worth knowing about, however: both in order to avoid unnecessary muddles, and for other reasons — taxonomic formalities are important in the politics of conservation, for instance.

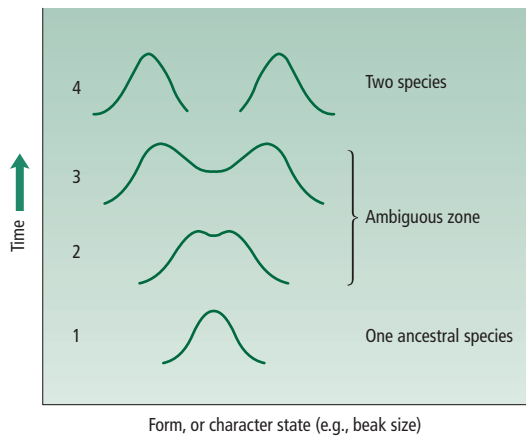
give a number of characters by which the two species can be told apart. In the adult, the bald eagle has a distinctive white head and tail, and a massive yellow bill. In North America, a bald eagle can therefore be recognized by the color of its feathers and bill. (Strictly speaking, the characters used to recognize species are often “diagnostic” rather than “defining” characters. Box 13.1 explains the distinction.)

In practice, the characters that define a species will not be present in all members of that species and absent from all members of other species. Nature is too variable. A perfectly defining character cannot usually be found, because the individuals of a species do not all look the same. One bald eagle will differ in color from another bald eagle. Real species form a “phenetic cluster”: the individuals in the species show a range of appearances, but they tend to be more similar to one another than to members of other species. Bald eagles tend to have one color pattern, golden eagles another. The defining characters are not perfectly discriminatory, but they do indicate how most members of the species differ from most members of other, related species.

In the most difficult cases, two species may blur into each other (Figure 13.2). Two species that only recently evolved from a common ancestor, or two populations that have not yet separated into two full species will be particularly likely to blur into each other. Ring species are an example (Section 3.5, p. 50, and Plate 1, opposite p. 68). In a ring species, two species appear to be present at one place, but those two “species” are connected by a series of forms that are geographically arranged in a ring. No phenetic character could be used, except arbitrarily, to divide the ring into two species. Such a

Interindividual variation causes problems

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**Figure 13.2**

Difficulties in species recognition are expected in the theory of evolution, because variation exists within each species and new species evolve by the splitting of ancestral species. During the evolution of new species, the distinction between the species will be ambiguous during times 2 and 3. At stage 3, for instance, no phenotypic character can unambiguously distinguish between two species; indeed two species do not yet exist.

The evolutionary controversies about species are not mainly concerned with practical or formal issues

division of the ring would also be theoretically meaningless: there really is a continuum, not a number of clear-cut, separate species. Problems of this kind are exactly what we should expect given that species originated by an evolutionary process. We should not expect clear-cut defining characters to exist for all species; that is not the way nature is.

Species are in practice mainly recognized by phenetic characters, more or less successfully. However, when evolutionary biologists discuss species concepts, they are not usually discussing how species are recognized in practice. They are discussing deeper, theoretical concepts of species, concepts that may lie beneath the practical procedures that are used to recognize particular species. Is the bald eagle just the set of eagles that have white heads and tails? Imagine that a parental pair of bald eagles with good white heads and tails produced a nest of eagles of some different color pattern. Would they have given birth to a new species? If the color of the head and tail was all there was to being a member of *Haliaeetus leucocephalus*, then the answer would clearly be yes. However, if the species have a more fundamental definition, and the coloration was picked only as a practically useful marker, then the answer would be no. Indeed, the new eagles without the white coloration would render that taxonomic character out of date, and it would be time to start looking for some other characters to recognize the species. Most of the discussion of species concepts that follows assumes that species definition has some deeper meaning than the phenetic characters used to recognize the species in practice. When biologists argue about species concepts they are not arguing about how species are defined in practice.



13.2 Several closely related species concepts exist

A first distinction among species concepts is between horizontal and vertical concepts (Figure 13.3). A horizontal concept aims to define which individuals belong to which species at any instant in time. A vertical concept aims to define which individuals belong to which species at all times. Vertical concepts are mentioned here mainly for completeness; most of the interest in species concepts is in horizontal concepts.

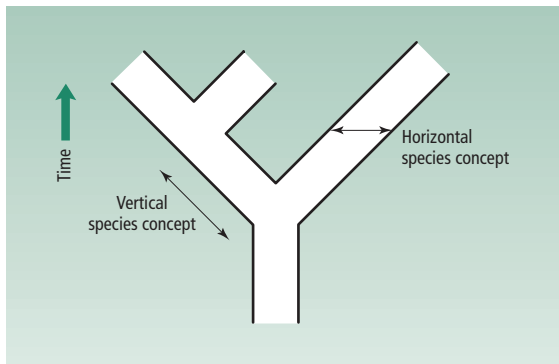


Figure 13.3

Horizontal and vertical species concepts. A horizontal concept aims to define species at a time instant and specifies which individuals belong to which species at one time. A vertical concept aims to define species through time and specifies which individuals belong to which species through all time.

Biologists are mainly concerned with defining species in the present, and this requires a horizontal concept. We need to know which eagles are *Haliaeetus leucocephalus* now, and are less interested in eagles a million years in the past or the future. This chapter concentrates on horizontal concepts.

13.2.1 *The biological species concept*

Species may be defined by interbreeding

The *biological species concept* defines species in terms of interbreeding. Mayr (1963), for instance defined a species as follows: “species are groups of interbreeding natural populations that are reproductively isolated from other such groups.” The expression “reproductively isolated” means that members of the species do not interbreed with members of other species, because they have some attributes that prevent interbreeding. The species concept that is now called the biological species concept actually predates Darwin — it was the species concept used by John Ray in the seventeenth century, for instance — but it was strongly advocated by several influential founders of the modern synthesis, such as Dobzhansky, Mayr, and Huxley, and it is the most widely accepted species concept today, at least among zoologists.

The biological species concept is important because it places the taxonomy of natural species within the conceptual scheme of population genetics. A community of interbreeding organisms make up, in population genetic terms, a gene pool. In theory, the gene pool is the unit within which gene frequencies can change. In the biological species concept, gene pools become more or less identifiable as species. The identity is imperfect, because species and populations are often subdivided, but that is a detail. The species, in this concept, is the unit of evolution. Organisms do not evolve but species do, and higher taxonomic groups such as phyla only evolve in so far as their constituent species are evolving.

The biological species concept explains why the members of a species resemble one another, and differ from other species. When two organisms breed within a species, their genes pass into their combined offspring; as the same process is repeated every generation, the genes of different organisms are constantly shuffled around the species gene pool. Different family lineages (of parent, offspring, grandchildren, and so on) soon become blurred by the transfer of genes between them. The shared gene pool gives

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Interbreeding explains why the members of a species resemble one another

the species its identity. By contrast, genes are not (by definition) transferred to other species, and different species therefore evolve a different appearance. The movement of genes through a species by migration and interbreeding is called *gene flow*. According to the biological species concept, gene flow explains why each species forms a phenetic cluster.

Moreover, the constant shuffling around of genes sets up a selection pressure favoring genes that interact well with genes at other loci to produce an adapted organism; a gene that does not fit in with the workings of other genes will be selected against. When we look at organisms today, we are looking at the effects of selection in the past. We should expect to see genes that interact well together within a species. The same is not true of genes in two separate species. These genes have not been tried out together and sifted by selection, and we have no reason to expect them to interact well. When combined in a single body, they may produce a genetic snarl-up. (Section 14.4, p. 389, further develops the theory of gene interactions within, and between, species.) Sexual interbreeding within a species produces what Mayr (1963) calls “cohesion” (and others call “cohesiveness”) in the species’ gene pool.

And how, in this concept, should the taxonomist’s method of defining species be interpreted? Taxonomists actually identify species by morphology, not interbreeding. On the biological species concept, the taxonomist’s aim should be, as far as possible, to define species as interbreeding units. The justification for defining species morphologically is that the morphological characters shared between individuals are indicators of interbreeding. When taxonomists can study interbreeding in nature they should do so and define the arrays of interbreeding forms as species. With dead specimens in museums, taxonomists should use the interbreeding criterion to guide their analysis of morphological criteria. Taxonomists should seek morphological criteria which define a species as a set of forms that appears to have the kind of variation that an interbreeding community would have. The morphological characters of species are then indicators of interbreeding, as estimated by the taxonomist. Eagles with white heads and tails are one interbreeding unit; eagles with the color pattern of the golden eagle are another.

The recognition concept defines species in terms of mate recognition

A closely related species concept is the *recognition species concept* of Paterson (1993). Paterson defines a species as a set of organisms with a shared specific mate recognition system (SMRS). The specific mate recognition system is the sensory method by which organisms recognize potential mates. For example, as many as 30 or 40 different species of crickets may be breeding within a single habitat in the USA. The male crickets broadcast their songs and are approached by females. Interbreeding is confined within a species because each species has its own distinctive song and females only approach males that are singing their species song. The system of a male song and a female acoustic system that leads females to approach some songs and not others is an example of what is meant by an SMRS. The set of organisms that are defined as a species by the biological and recognition species concepts will be very similar, because organisms that interbreed will usually also have a shared SMRS.

Another closely related concept has been developed to make use of the increasing quantities of data from molecular genetic markers, which can be used to recognize which sets of organisms belong to the same evolutionary lineage (Howard & Berlocher 1998). In all, several species concepts exist that are inspired by the underlying idea that species exist because of interbreeding among the individual organisms within each

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species. The biological species concept is the most influential of these reproductive species concepts.

13.2.2 *The ecological species concept*

Species may be defined ecologically, by a shared ecological niche

The forms and behavior of organisms are, at least to some extent (Chapter 10), adapted to the resources they exploit and the habitats they occupy. According to the *ecological species concept*, populations form the discrete phenetic clusters that we recognize as species because the ecological and evolutionary processes controlling how resources are divided up tend to produce those clusters. About half a century of ecological research, particularly with closely related species living in the same area, has abundantly demonstrated that the differences between species in form and behavior are often related to differences in the ecological resources the species exploit. The set of resources and habitats exploited by the members of a species form that species' ecological niche and the ecological species concept defines a species as the set of organisms exploiting a single niche. (In some cases, a full definition would have to be more long-winded. If, for instance, the juvenile stage of an organism lives in plankton while the adult stage is attached to rocks, then the different life stages exploit different ecological niches. However, the definition could be expanded to define a species as a set of organisms who exploit a certain set of niches, where the set includes the niches exploited by different life stages, genders, or other forms within the species.)

Why should ecological processes produce discrete species? Parasite–host relations provide a clear example. Imagine the parasites exploiting two host species. The host species will differ in certain respects, perhaps in where they live, or the times of day they are active, or their morphology. The parasites will evolve appropriate adaptations to live in one or the other host. The parasites then tend to become two discrete species, because their environmental resources (hosts in this case) come in two discrete kinds.

The ecological force of competitive exclusion maintains species differences

Two host species can clearly provide two discrete sets of ecological resources. But in other cases, the ecological resources may not come in such discrete units. Consider, for example, the five species of warblers in Maine that were the subject of a classic study by MacArthur (1958). MacArthur showed that each species mainly exploited a particular subregion of the trees they all lived in. Some species foraged higher, some lower; some foraged near the ends of branches, others nearer the center of the tree. These variables, like height in tree, are continuous. The warblers form five distinct, discrete species, but they divide up resource variables that are continuous. In this case, an ecological explanation for the existence of discrete species mainly comes from the principle of *competitive exclusion*. Only species that are sufficiently different can coexist. The result is that even with a continuous resource distribution, species may evolve into a series of discrete forms along the continuum. If the species blurred into one another, superior competitors could drive inferior competitors extinct, and gaps between species would appear. (The theory of speciation (Chapter 14) suggests some further reasons why discrete species evolve on continuous resources. Also, Section 13.7.2 discusses further evidence that ecological factors influence the array of phenetic forms in a species.)

The ecological and biological species concepts are closely related. Life, according to the ecological species concept, comes in the form of discrete species because of

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adaptation to exploit the resources in nature. Interbreeding is shaped by the same process. Natural selection will favour organisms who interbreed with other organisms that have a similar set of ecological adaptations. For instance, the ecological adaptation might be the size of the beak, if the beak is adapted to eat seeds found locally. Natural selection favors individual birds that interbreed with other birds that have similar beaks. Then they will on average produce offspring that are well adapted to eat the local seeds. Natural selection works against birds that interbreed with mates that have very different beaks as their offspring will tend to have maladapted beaks. The patterns of interbreeding and the ecological adaptations in a population are therefore shaped by common evolutionary forces. Notwithstanding the close relations between the concepts, some controversy still exists between them (Section 13.7 below).

13.2.3 *The phenetic species concept*

Species may be defined by shared phenetic attributes

The phenetic species concept can be understood as an extension of the way taxonomists define species (Section 13.1). Taxonomists define each species by a particular defining character, or characters, that is shared by its members. In general we could define a species as a set of organisms that are phenetically similar, and distinct from other sets of organisms. This would be a “phenetic” species concept: it defines species in general by shared phenetic attributes. One noteworthy feature of the phenetic concept is that it is not based on a theory of why life is organized into discrete species. The biological and ecological concepts are both theoretical, or explanatory, concepts. They define species in terms of processes that are thought to explain the existence of species: interbreeding or ecological adaptation. The phenetic species concept is non-theoretical, or descriptive. The concept simply notes that species do in fact exist, in the form of phenetic clusters. Why species exist in this form is a separate question.

The classic version was the typological, . . .

The classic version of the phenetic species concept is the “typological species concept” (the term “morphological species concept” has also been used to refer to much the same concept). The word “typological” comes from the word “type,” which is used in formal taxonomy. When a new species is named, its description is based on a specimen called the type specimen, which has to be deposited in a public collection. According to the typological species concept, a species consists of all individuals that look sufficiently similar to the type specimen of the species. We shall look further at “typological thinking” in Section 13.5, where we shall see why typology is thought to be invalid in modern evolutionary theory.

. . . a later version was the numerical, . . .

A later version of the phenetic concept was developed by the school of numerical taxonomy in the 1960s. (On numerical taxonomy, see Section 16.5, p. 476.) Numerical taxonomists developed statistical techniques for describing the phenetic similarity of organisms. Those techniques could be applied to recognize species. A species could then be defined as a set of organisms of sufficient phenetic distinctness (where the word “sufficient” could be made precise by the statistical methods used to describe phenetic similarity). The numerical taxonomists’ phenetic species concept has nothing to do with the typological concept, but belongs to the same family of concepts.

Some versions of a more recently proposed *phylogenetic species concept* also define species by a kind of phenetic similarity. For instance, Nixon & Wheeler (1990) define a

... and there are other, modern, phenetic species concepts

species as “the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals.”

The various phenetic species concepts are closely related to the biological and ecological concepts. All these concepts will recognize much the same species in nature. A set of organisms that are adapted to a similar niche are likely to be phenetically similar, because they share a set of phenetic characters that are used to exploit the ecological resources. A set of organisms that interbreed are also likely to be phenetically similar. The ancestors of the modern members of the species have interbred, resulting in genetic (and therefore phenetic) similarity among the members of the species now. In Section 13.7 we look at controversies among species concepts. It will be worth keeping in mind that all the concepts agree most of the time both about what species exist in nature and about what the biological forces are that explain those species.

13.3 Isolating barriers

13.3.1 *Isolating barriers prevent interbreeding between species*

Isolating barriers evolve between species

Why is it that closely related species, living in the same area, do not breed together? The answer is that this is prevented by *isolating barriers*. An isolating barrier is any evolved character of the two species that stops them from interbreeding.² The definition specifies “evolved characters” to exclude non-interbreeding due to simple geographic separation. Interbreeding between two geographically separate populations of a species is impossible, but the geographic separation is not an isolating barrier in the strict sense. Geographic separation alone does not have to be an evolved character, and is unlikely to be an evolved character when it is between two populations of a species. One subpopulation can colonize a new area without any genetic change, or the populations may have been separated by a geographic accident, such as the formation of a new river. Courtship, however, is an example of an isolating barrier. If two species do not interbreed because their courtship differs, then the courtship behavior of at least one of those species must have undergone evolutionary change.

There are several kinds of barrier

Several kinds of isolating barrier are distinguished; Table 13.1, based on Dobzhansky (1970), gives one classification. The most important distinction is between prezygotic and postzygotic isolation. Prezygotic isolation means that zygotes are never formed, for instance because members of the two species are adapted to different habitats and never meet, or have different courtships and do not recognize each other as potential

² What is here called an “isolating barrier” has until recently (following Dobzhansky (1970)) usually been called an “isolating mechanism.” Some biologists have criticized the word “mechanism” because it might imply that the character that causes isolation evolved in order to prevent interbreeding — that the isolating mechanism is an adaptation to prevent interbreeding. As we shall see in Chapter 14, the characters that cause reproductive isolation certainly sometimes, and perhaps almost always, evolve for other reasons and prevent interbreeding only as an evolutionary by-product. The use of the term “isolating barrier” is becoming common now, and I follow this usage. However, the older expression could be defended. In biology, a mechanism of *X* is not always something that evolved to cause *X*. Compare, for instance, “population regulation mechanism,” “mechanism of mutation,” “mechanism of speciation,” and “mechanism of extinction.” Isolating mechanism could mean only a mechanism that isolates, not a mechanism that evolved in order to isolate.

Table 13.1

Dobzhansky's classification of reproductive isolation barriers. From Dobzhansky (1970).

1. *Premating or prezygotic* mechanisms prevent the formation of hybrid zygotes
 - (a) *Ecological or habitat isolation*. The populations concerned occur in different habitats in the same general region
 - (b) *Seasonal or temporal isolation*. Mating or flowering times occur at different seasons
 - (c) *Sexual or ethological isolation*. Mutual attraction between the sexes of different species is weak or absent
 - (d) *Mechanical isolation*. Physical non-correspondence of the genitalia or the flower parts prevents copulation or the transfer of pollen
 - (e) *Isolation by different pollinators*. In flowering plants, related species may be specialized to attract different insects as pollinators
 - (f) *Gametic isolation*. In organisms with external fertilization, female and male gametes may not be attracted to each other. In organisms with internal fertilization, the gametes or gametophytes of one species may be inviable in the sexual ducts or in the styles of other species
2. *Postmating or postzygotic* isolating mechanisms reduce the viability or fertility of hybrid zygotes
 - (g) *Hybrid inviability*. Hybrid zygotes have reduced viability or are inviable
 - (h) *Hybrid sterility*. The F₁ hybrids of one sex or of both sexes fail to produce functional gametes
 - (i) *Hybrid breakdown*. The F₂ or backcross hybrids have reduced viability or fertility

mates. Alternatively, the members of two species may meet, mate, and form zygotes, but if the hybrid offspring are inviable or sterile then the two species have postzygotic isolation.

13.3.2 *Sperm or pollen competition can produce subtle prezygotic isolation*

Over evolutionary time, differences accumulate between species and the result is that they become fully isolated by both prezygotic and postzygotic isolating barriers. They will evolve different appearances, different courtships, different ecological adaptations, and different and incompatible genetic systems. However, closely related and recently evolved species may be only partly isolated, and then research can reveal which isolating barriers are at work.

Gametic isolation is a kind of isolating barrier . . .

One factor that has been investigated recently in several species is “gametic isolation” (Table 13.1). The simplest kind of gametic isolation occurs when the sperm and eggs of two species do not fertilize each other. But a process called “sperm competition” can cause a subtler kind of gametic isolation. Two species may not interbreed because the sperm, or pollen, of species 1 outcompetes that of species 2 when fertilizing the eggs of species 1, but the sperm, or pollen, of species 2 outcompetes that of species 1 when fertilizing the eggs of species 2. Wade *et al.* (1993), for instance, studied reproductive isolation between two beetles, *Tribolium castaneum* and *T. freemani*. *T. castaneum*

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is a worldwide pest of stored flour called the flour beetle, and *T. freemani* is a closely related species that lives in Kashmir. The two species are not isolated at the premating stage: males of both species copulate indiscriminately with females of both species. Wade *et al.* quote a remark about the mating propensities of male flour beetles, who “will attempt copulation with other males, dead beetles of both sexes, or with any object, such as a lump of flour or frass, which looks like a beetle.”

... that has been shown by recent experiments

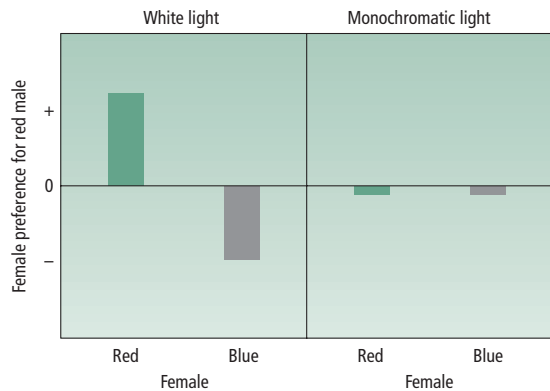
Wade *et al.* (1993) did an experiment in which they put female *T. freemani* in one of three situations: (i) with two successive males of *T. freemani*; (ii) with two successive males of *T. castaneum*; or (iii) with one male *T. freemani* and then one male *T. castaneum*. The female beetles laid a similar number of eggs in all three cases, and a similar percentage of the eggs hatched and grew up (though the interspecies hybrid offspring are sterile). This shows that the sperm of male *T. castaneum* are capable of fertilizing *T. freemani* eggs. When female *T. freemani* were put with males of both species (condition (iii)), less than 3% of the offspring were hybrids — over 97% of the eggs had been fertilized by the *T. freemani* male's sperm. The reason is that when two males inseminate the same female, their sperm compete inside the female to fertilize her eggs. In this case, when no *T. freemani* sperm are present, *T. castaneum* sperm can fertilize the eggs, but when *T. freemani* sperm are present they outcompete the *T. castaneum* sperm. Sperm competition is causing reproductive isolation. (Sperm competition is a form of sexual selection, discussed in Section 12.4, p. 327. It is a form of male competition, and its outcome may well be influenced by female choice. In this case, the “choice” would be effected by the female's internal reproductive physiology. Section 14.11, p. 413, discusses how sexual selection may contribute to speciation, and provides further contexts for these observations.)

The experiment matters not only for revealing the nature of reproductive isolation in this pair of beetles, but also shows what needs to be done in research on prezygotic isolation. An experiment in which males of one species are simply crossed with females of another species is inadequate to measure prezygotic isolation. When male *T. castaneum* are put with female *T. freemani* they produce hybrid offspring. We might falsely conclude that these two species are not prezygotically isolated. But if the females are put with male *T. freemani* and *T. castaneum*, hardly any hybrid offspring are produced and the prezygotic isolation is revealed. Isolation by sperm, or pollen, competition has recently been found in many species (Howard 1999).

13.3.3 **Closely related African cichlid fish species are prezygotically isolated by their color patterns, but are not postzygotically isolated**

Cichlid fish are found globally in warm freshwater environments, but they are famous for the huge numbers of species that have evolved in the East African lakes. They are also famous as a conservation disaster, as a large but unknown number of species have been lost following the introduction of a predatory fish, the Nile perch, into the lakes, together with increasing lake eutrophication. Here we concentrate on the reproductive isolation between two cichlid species that live in Lake Victoria.

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**Figure 13.4**

Mating preferences (a form of prezygotic isolation) in two cichlid species from Lake Victoria, Africa. The two species are referred to as the “red” and “blue” species: see text for details and Plate 7 (between pp. 68 and 69) for illustration. Individual females of each species were given a choice of two males, one from each species. A preference for males of the red species was arbitrarily defined as a positive preference; a negative preference indicates a preference for males of the blue species. Females preferred conspecific males in normal white light, but the preference disappeared in monochromatic light, where the two species were visually indistinguishable. From Seehausen & van Alphen (1998).

Experiments show that cichlid fish are isolated by color pattern . . .

Cichlids often have beautiful color patterns, and *Pundamilia nyererei* and *P. pundamilia* are related species that differ in color (see Plate 7, between pp. 68 and 69). For simplicity, we can refer to *P. nyererei* as red and to *P. pundamilia* as blue, but the color illustrations show that the words red and blue hardly describe the gorgeous colors of the two species. Seehausen & van Alphen (1998) performed a laboratory experiment on the mating preferences of the two species. They first tested the preferences of females of both species for males of one species or the other, in normal light. The result was that the females of both species preferred conspecific males (Figure 13.4). The two species show prezygotic isolation by mating behavior. Seehausen and van Alphen then repeated the experiment, but in monochromatic light, in which the color difference between the two species was invisible (Plate 6). Now the females of both species show no preference between red and blue males. The experiment shows that the prezygotic isolation is due to the color patterns of the two fish species.

. . . and not postzygotically, . . .

Seehausen’s lab has also measured postzygotic isolation (Seehausen *et al.* 1997). The two species will interbreed in the lab and produce hybrids. The hybrids are fertile, and by 2001 five generations of hybrids had been successfully bred: the two species are not postzygotically isolated. In conclusion, *P. nyererei* and *P. pundamilia* are isolated prezygotically by color pattern but not postzygotically.

. . . which has consequences for the effect of pollution

The main point of Seehausen’s experiment here is to show how isolating barriers can be investigated, but the results have two other interests. One is in relation to conservation. The color differences between the two species become less visible in cloudy, eutrophic waters. Pollution in Lake Victoria is making it more likely that the two species hybridize. Pollution is leading to a loss of biodiversity, not by the normal mechanism of extinction but by removing the isolating barrier between closely related species. The other interest is in relation to speciation, and illustrates a similar point to the study of flour beetles. Mate preference, like sperm competition, is a form of sexual selection. Sexual selection is thought to drive speciation, particularly sympatric speciation (Section 14.11, p. 414). The African lake cichlids provide some of the strongest evidence for sympatric speciation (Section 14.10.3, p. 413). Seehausen’s experiments, which show that mating preferences are the first kind of isolation to evolve in these fish, fits in with the broad idea that sexual selection has contributed to the spectacular radiation of cichlids in East Africa.

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In conclusion, over evolutionary time the amount of isolation between two species will increase and the species will eventually be isolated by most of the barriers listed in Table 13.1. (Think of how humans are isolated from a distant species, such as a baboon — we are probably isolated from them by everything in the list except habitat and breeding season.) Experiments can be done to reveal what the particular isolating barriers are between closely related species. These experiments can reveal what isolating barriers are at work in the early stages of speciation. We return to this topic in Chapter 14.

13.4 Geographic variation within a species can be understood in terms of population genetic and ecological processes

Intraspecific variation exists both at any one place and between different places. If we sample a number of individuals belonging to one species at any one locality, those individuals may differ — variation within a population — often showing a normal distribution (Section 9.2, p. 226). Also, if we sample individuals belonging to one species, from different places, they may differ — variation between populations, or geographic variation.

We need to examine intraspecific variation both in order to understand the nature of species and also to understand how new species evolve. As Chapter 14 will discuss, the evolution of new species consists of the conversion of variation within one species into differences between species. Chapters 5–9 looked at the factors that control variation within a population: variation may be maintained by natural selection, or a balance of selection and mutation, or a balance of drift and mutation. Here we shall look at variation between populations (geographic variation), and its relation with variation within each population. (The theory in Section 5.14, p. 129 is related to the topic here.)

13.4.1 *Geographic variation exists in all species and can be caused by adaptation to local conditions*

Johnston & Selander (1971) measured 15 morphological variables in 1,752 house sparrows (*Passer domesticus*) sampled from 33 sites in North America. The 15 characters can be reduced to a single abstract character of “body size” (to be statistically exact, this character was the first principal component). In Figure 13.5 the average body size of house sparrows is plotted on a map and two things are immediately important.

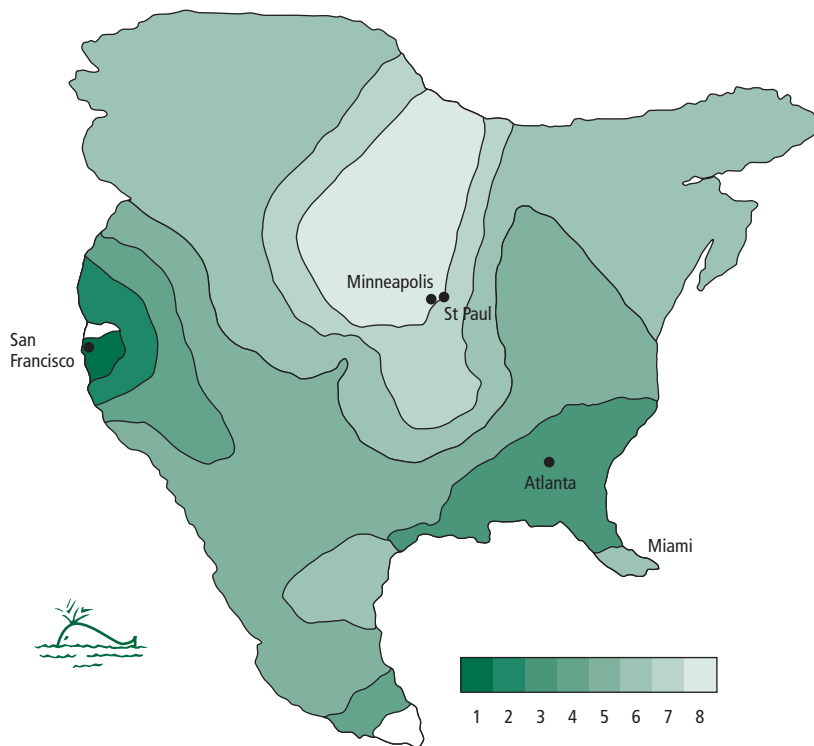
We have good evidence of geographic variation

First, and more important for our purposes, is simply that the characters vary in space: house sparrows from one part of the continent differ from those in other parts. Almost every species that has been studied in different places has been found to vary in some respect. Not all characters vary (for instance, humans have two eyes everywhere), but populations always differ in some characters. Different populations have been found to differ in morphology, in the amino acid sequences of their proteins, and the base sequence of their DNA. Geographic variation is ubiquitous. Mayr, most

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Figure 13.5

Size of male house sparrows in North America. Size is measured as a “principal component” score, derived from 15 skeletal measurements. The score of 8 is for the largest birds, the score of 1 is for the smallest. The study described in Section 3.2 (pp. 46–7) is a precursor of this research. Redrawn, by permission, from Gould & Johnston (1972), corrected from Johnston & Selander (1971). © 1972 Annual Reviews Inc.



powerfully in his book *Animal Species and Evolution* (1963, chapter 11), has collected more evidence about geographic variation than anybody else and he concludes that “every population of a species differs from all others,” and “the degree of difference between different populations of a species ranges from almost complete identity to distinctness almost of species level.”

Sparrows illustrate Bergman’s rule

The second point to notice in Figure 13.5 is that the form of the geographic variation is explicable. House sparrows are generally larger in the north, in Canada, than in the center of America. The generalization is imperfect (compare, for instance, the sparrows of San Francisco and Miami); but in so far as it applies, it illustrates *Bergman’s rule*. Animals tend to be larger in colder regions, presumably for reasons of thermoregulation. Geographic variation in these two species is therefore adaptive: the form of the sparrows differs between regions because natural selection favors slightly differing shapes in different regions.

13.4.2 Geographic variation may also be caused by genetic drift

House mice (*Mus musculus*) have a standard diploid chromosomal set of 40 chromosomes ($2N = 40$). The centromeres of all 20 chromosomes are near the chromosomes ends and, perhaps for this reason, chromosomal fusions often take place in this species. In a chromosomal fusion, two chromosomes join together at their terminal

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centromeres. They form a new, longer chromosome with its centromere nearer the center. A fused chromosome often becomes established in a local population of house mice. The result is that the local population has less than 40 chromosomes per mouse.

Geographic variation in mice chromosomes . . .

Britton-Davidian *et al.* (2000) described a remarkable example recently, in the mice on the island of Madeira (see Plate 8, between pp. 68 and 69). They found that different chromosomal fusions were fixed in local mouse populations only 5–10 km apart. One local population might have 28–30 chromosomes per mouse, because five or six chromosomal fusions had occurred. In another population, three further fusions reduced the numbers to $2N = 22$. According to Britton-Davidian *et al.* “house mice are thought to have been introduced onto Madeira following the first Portuguese settlement during the fifteenth century.” If this is correct, the geographic variation illustrated in Plate 8 has all evolved in under 500 years. Mice, and rodents generally, show rapid chromosomal evolution. By way of contrast, all human populations have the same set of chromosomes, except for rare mutants.

. . . looks like an example of genetic drift . . .

What is the cause of this chromosomal evolution? The answer is uncertain, but it is thought to be random drift. A mouse containing a fused chromosome contains the same genes as a mouse with the two separate chromosomes. The mouse may grow up identically either way. However, a chromosomal mutation will initially exist in heterozygous form, and such heterozygotes tend inherently to be disadvantageous. A fusion between chromosomes 1 and 2 can be represented as 1+2. The heterozygote can be written 1,2/1+2. The heterozygote is disadvantageous during cell division, particular meiosis. For instance, the fused chromosome 1+2 may pair with chromosome 1, leaving chromosome 2 unpaired. The unpaired chromosome 2 may then segregate with chromosome 1, producing viable offspring. Or it may be segregated with chromosome 1+2, producing offspring with too many, or too few, chromosomes.

When a new chromosomal fusion mutation arises, it will be selected against because of its disadvantage in heterozygous form. But if it drifts up to a locally high frequency, as may easily happen in a local, small, and perhaps inbreeding, mouse population, natural selection will favor it. Natural selection favors whichever chromosomal form is locally common (this is an example of positive frequency-dependent selection, Section 5.13, p. 127). Natural selection alone cannot explain the geographic variation observed by Britton-Davidian *et al.* Natural selection alone would cause all the mice to have the same chromosome numbers. The variation is more likely to be explained by drift, with different individual chromosomal fusions drifting up in frequency in different localities. Natural selection may also be at work, depending on the frequency of the chromosomes. But whatever the cause of the pattern in Plate 8, it is a further example of geographic variation.

. . . though other factors may contribute

Geographic variation is probably rarely caused only by drift or only by selection. Also, more than one selective factor is likely to operate. In the case of the mouse chromosomes, natural selection probably interacts with drift, depending on the chromosomes' frequency. But other kinds of natural selection can act, such as meiotic drive (Section 11.2.1, p. 294) and a full account of mouse chromosomal evolution is complex (Nachman & Searle 1995). Moreover, very thorough research is needed to test between selection and drift.

Linanthus parryae is a small desert flower, living on the edge of the Mojave Desert in California. Local populations vary according to the frequency of the white and blue

flowers. Wright (1978) considered it to be the best example of how drift causes differences between local populations (the first stage in Wright’s shifting balance theory of evolution — see Section 8.13, p. 216). However, a long-term study by Schemske & Bierzychudek (2001) measured the fitness of blue and white flowers and found that selection is at work in a complex way that differs from year to year. A small study, over 1 or 2 years, might have supported Wright’s interpretation but Schemske and Bierzychudek counted more than 710,000 seeds from more than 42,000 flowers over an 11-year period and they have effectively refuted drift as the explanation of variation in this particular species.

Hard work is needed to measure the contributions of drift and selection in particular species. But in general, patterns of geographic variation can be explained by some mix of selection, as seems to explain body size variation in sparrows, and of drift, as seems to explain chromosomal variation in house mice.

13.4.3 Geographic variation may take the form of a cline

A cline is a continuous gradient of variation, within a species

If we drew a line on Figure 13.5 from Atlanta to Minneapolis and St Paul, or from the twin cities to San Francisco, and looked at the size of sparrows along it, we should have an example of a cline. A *cline* is a gradient of continuous variation, in a phenotypic or genetic character, within a species. Clines can arise for a number of reasons. In the house sparrows, the reason is likely that natural selection favors a slightly different body size along the gradient; sparrows are continuously adapted to an environment that changes continuously in space (Figure 13.6). For instance, body size may be adapted to environmental temperature. Temperature gradually decreases to the north, and body size in the sparrows increases as we go north. Alternatively, the environment may change discontinuously in space and different genes may be adapted to the two regions (Figure 13.6b). A cline can then arise because of gene flow: the movements of individuals, or their pollen in the case of plants.

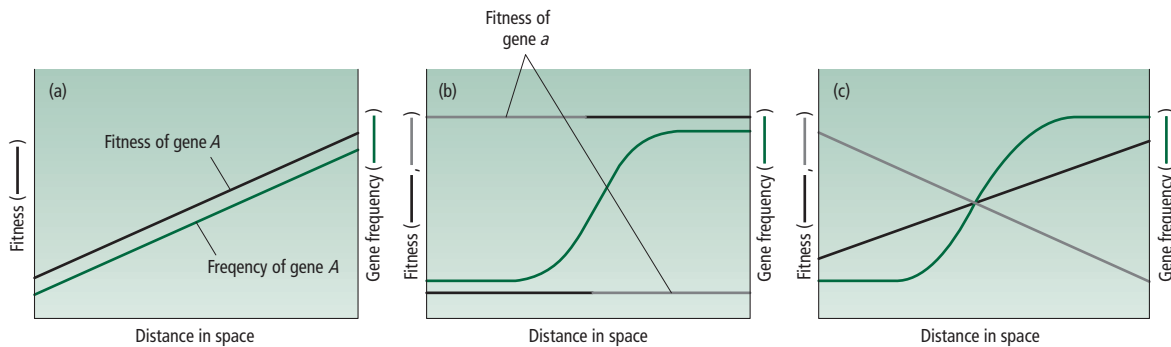


Figure 13.6

A cline can arise in various forms. (a) It can occur in a continuous environmental gradient. The house sparrow example (see Figure 13.5) probably has polygenic inheritance; the y-axis would more appropriately express the proportion of

genes for larger body size than the average for the USA. (b) A cline can also arise when natural selection favors different genotypes in different discrete environments and there is gene flow (migration) between them. (c) A situation like (b) except that the environment changes gradually rather than suddenly.

In a stepped cline, the gradient is less smooth

Clines may be smooth or “stepped” (Figure 13.6c), depending on how suddenly gene frequencies change in space. If the environment varies smoothly, the cline will also be smooth. If the environment changes more suddenly, the cline may be more stepped. The shape of the step depends on the fitness difference between the genotypes in the two regions, the fitness of any intermediate genotypes (such as heterozygotes or recombinants), and the amount of gene flow. A sudden change in the environment is called an “ecotone” (Section 13.7.2 below contains an example from the grass *Agrostis*). However, ecotones are not the only explanation for stepped clines. Stepped clines may also result when the ranges of two formerly separate populations expand and the two populations meet up (Section 17.4, p. 500). Or they may result from genetic drift. When biologists see a stepped cline, they are interested to know whether it corresponds with an ecotone or has some other explanation. The main point here, however, is that geographic variation often takes the form of a cline. Clinal variation contrasts with a case such as that of the mice of Madeira, where the local populations do not show a gradient of variation.

13.5 “Population thinking” and “typological thinking” are two ways of thinking about biological diversity

Mayr distinguished population from typological thinking

Species show variation, both between individuals at any one place (often this has the form of a “bell curve” or normal variation) and geographic variation between individuals from different places. This variation has been thought about in two main ways: “population thinking” and “typological thinking” (Mayr 1976). We have already met the typological species concept (Section 13.2.3). A “type” specimen has to exist in order for a species to be defined. However, variation will exist in the species with some individuals more like the type specimen, and others less like it. By typological thinking, Mayr meant the idea that the type individual, and other individuals like it, are in some sense “better” examples of their species — they are more real, or more representative, members of their species. We can see what this means if we think about the classification of many non-biological entities.

Typological thinking is often appropriate outside biology

Suppose we are classifying objects as chairs or non-chairs. Some objects will be better specimens of chairs than others. If an object has four equal length legs and a horizontal surface to sit on, it is a “good” chair. By calling something a good chair, or a better specimen of a chair, we mean that it is easily recognized as a chair, not that it is morally superior to other objects that are less easily recognized as chairs. Some other object may look rather like a chair, but have two legs missing and a third broken, making it less representative of the category of chairs. Other objects may be so smashed up that we might hesitate to call them chairs at all. The variation between objects consists of some objects that are good chairs, and others that are less good chairs. The “less good” chairs mainly exist because of some kind of accident or environmental error, such as an accident in which a leg is broken off. We think to some extent typologically about chairs: some entities are typical chairs, others are less typical because there is something wrong with them.

Creationism could give an account of biological species that is rather like the typological account of chair classification. Each species might have a “best” form, perhaps

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Typological thinking is inappropriate in biological classification

corresponding to the optimal adaptation for the local environment. Individuals that deviated from that optimum might be less clearly recognized as members of their species; and they are also adaptively inferior. They might deviate from the optimum because of mutational error, or environmental accidents, that carried the phenotype away from the optimum.

Typological thinking means dividing variation into good, type specimens that are more real members of their category, and accidental deviants that are less good members of the category. The example we have just looked at, in terms of optimal adaptation and mutational and environmental error, is only one version of typological thinking. Historically, typological thinking has been based on ideas that no longer look scientific. For instance (in an extreme case) the nineteenth century taxonomist Louis Agassiz said that species are thoughts in the mind of God. The “good” specimens of the species, near the type specimen, would then exactly correspond to God’s thoughts and the other specimens, away from the center of the bell curve, would be inferior approximations. *Any* theory in which some versions of a species are better representatives of that species than are other versions is likely to be a case of typological thinking.

Both selection . . .

In modern evolutionary thinking, however, variation is non-typological. All the individuals of a species are equally good specimens of that species and they are equally representative of it. The species does not have some individuals that are more typical of it than others. We can see the case for population thinking in the evidence for geographic variation. Sparrows vary in size through North America: the variation is partly due to temperature differences between places, with sparrows evolving larger sizes where it is colder. It is not true that one size of sparrow is better, or more real, or more representative of sparrowness, than any other size within the species’ range. All the sparrows are equally good sparrows.

. . . and drift . . .

The same can be said about the chromosomal forms of mice, if they are indeed caused by genetic drift. One chromosomal form is as good as another. The variation is neutral, and no one form of mouse can be recognized as a truer type of mouse than the others. Even if the variation within a species is partly due to mutation–selection balance (and some individuals are better adapted than others), the environment could change and the currently less fortunate individuals would improve in fitness. That is how evolutionary change occurs. Variation is essential for the evolutionary process. It is true that one individual of the species is used to define each species, and that individual is called the type specimen; but the use of type specimens is now just a legalistic naming procedure. It does not imply that individuals with the exact set of characters used to define the species are in any way better or more representative members of the species than are other individuals who happen to have variant forms of the defining characters.

. . . cause biological populations to show variation

Mayr (1976) argued that the replacement of typological by population thinking was one of the key features of the Darwinian revolution. And the main point here has been that population thinking makes more sense than typological thinking given what we understand about evolution. However, the distinction has some wider implications. Typological thinking can easily complement racist or other illiberal ideologies in which some humans, or kinds of humans, are regarded as superior, or fuller, specimens of humanity than are others. Box 13.2 looks at human variation, and at evidence that humans have an exceptionally low amount of interracial difference relative to other species.



Box 13.2 Human Variation and Human Races

Imagine a species made up by a number of geographic populations. How can we describe the amount of genetic divergence between the local populations? A number of statistics exist, of which G_{ST} is one of the clearest.

$$G_{ST} = \frac{H_T - H_S}{H_T}$$

H stands for heterozygosity (Box 6.3, p. 149); the subscript “S” implies subpopulation and “T” implies total population. We can see how G_{ST} behaves by looking at two extreme cases. Imagine first a case of maximal geographic divergence. Imagine there are two local populations, equal in size, and allele A is fixed in one and allele a is fixed in the other. We first compute the heterozygosity of the total population (H_T). Because the two subpopulations are equal in size, the gene frequency of A is 0.5, and of a is 0.5: $H_T = 0.5$. We now compute the heterozygosity in each subpopulation (H_S). Only one allele is present in each case and $H_S = 0$. $G_{ST} = (0.5 - 0)/0.5 = 1$.

Now imagine that the same two alleles are present, but the two local subpopulations are identical. The frequency of A is 0.5 and of a is 0.5 in both populations. H_T again is 0.5 because the gene frequencies are 0.5 in

the combined population as a whole. H_S also is 0.5 within each subpopulation. $G_{ST} = (0.5 - 0.5)/0.5 = 0$. With no genetic divergence between local populations, G_{ST} is 0; with complete divergence, G_{ST} is 1; with intermediate levels of divergence, G_{ST} has a value between 0 and 1.

What values does G_{ST} have for real species? Table B13.1 lists some figures. We can notice two features. One is that different species show a range of degrees of divergence between local populations. The other is that the figure for humans is low, relative to the majority of other species; the genetic difference between the major human races is lower than for the geographic races of most other species. The figure of $G_{ST} = 0.07$ means that 93% of human genetic variation is present within each racial group. Only 7% of human genetic variation is due to genetic differences between races. The figures in Table B13.1 are based on protein data, but much the same results have been obtained with human DNA (Barbujani *et al.* 1997). DNA data, however, are not available for enough species to enable an interspecies comparison possible.

Why is racial divergence relatively low in humans as compared with other species? The answer is unknown, but one reason may be that the human

Table B13.1

The fraction of genetic variation within, and between, races of a species, as expressed in the statistic G_{ST} . From data in Crow (1986).

Species	G_{ST}
Horseshoe crab	0.07
Humans	0.07
<i>Drosophila equinox</i>	0.11
Mouse	0.12
Club moss	0.28
Kangaroo rat	0.67

species has evolved only recently. All modern humans may share a common ancestor who lived in Africa as recently as 100,000 years ago (and at any rate less than 500,000 years ago). The genetic differences between human races have accumulated since then. Maybe human races are too recent for much genetic difference to have evolved. In other species, races may have been longer established and G_{ST} has built up to a larger number. Whatever the interpretation, G_{ST} and the other statistics like it provide useful ways of describing geographic variation within a species.

Further reading: Cavalli-Sforza (2000).

In summary, we have seen two concepts of intraspecific variation. One is typological, and supposes that some individuals within a range of variation are better representatives of a species than are other individuals. The other concept is population thinking and treats variation as real and important: no one individual within the range of variation is privileged in any way and all specimens are equally good members of a species.

13.6 Ecological influences on the form of a species are shown by the phenomenon of character displacement

Ecological competition can influence the form of a species (as we mentioned, theoretically, in Section 13.2.3 above). The range of a morphological character, such as beak size, within a species may be limited because the extreme forms suffer competition from neighboring species. In this section we shall look at some evidence for the influence of ecological competition on species. The clearest evidence is provided by *character displacement*.

Two species may differ more in places where they coexist than elsewhere

Character displacement can arise in the following conditions. Two closely related species exist — species that may be ecological competitors. The two species must have a special kind of geographic distribution: it must be the case that both species are present in some places, but only one of the species is present at other places. That is, the two species must have partly overlapping ranges. Character displacement means that individuals of the two species differ more if they are sampled from a place where both species are present (*sympatry*, same place) than do individuals sampled from places where only one of the species is present (*allopatry*, other place). In these terms, character displacement means that sympatric populations of two species differ more than do allopatric populations of the same two species.

Character displacement is difficult to detect because it requires two competing species to have partly overlapping ranges. Many pairs of species either have completely separate ranges, or ranges that are very similar; in either case, it is impossible to study character displacement.

Two salamander species are an example

An example of character displacement comes from two species of salamander, *Plethodon cinereus* and *P. hoffmani*. *P. cinereus* lives throughout much of northeastern USA, except for parts of Pennsylvania and Virginia, whereas *P. hoffmani* lives in parts of Pennsylvania where *P. cinereus* is absent. The two species also live together, sympatrically, in a small region of overlap in Pennsylvania. The two species differ in the shape of their heads and jaws: *P. hoffmani* has a jaw that is relatively weak but can be closed fast and *P. cinereus* has a stronger jaw but is slow to snap it shut. *P. hoffmani* is better adapted to eat large prey items, which are caught by immediately closing the mouth on them, whereas *P. cinereus* is better adapted to eat smaller prey, which are eaten by pressing them between the tongue and teeth.

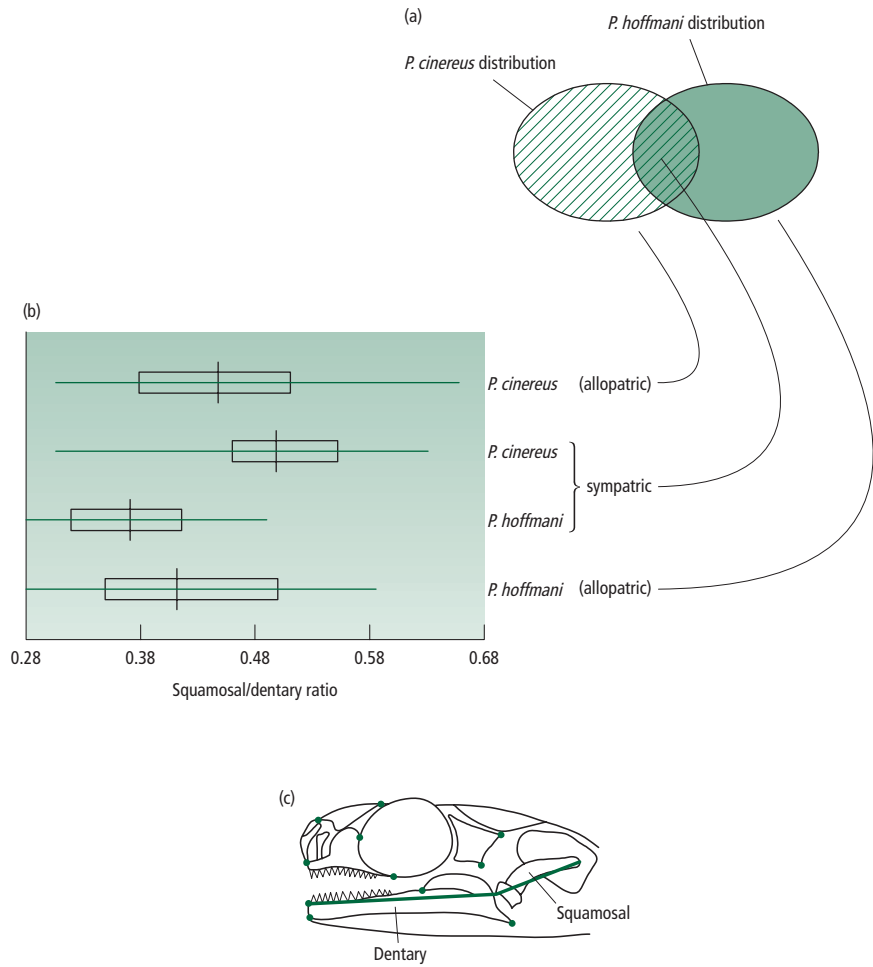
Figure 13.7 shows that the two species differ more in locations where both species are present, that is they show character displacement. The standard interpretation of character displacement is that, where only one species is present, it is released from competition with the other species and it evolves to exploit resources that would be taken by its competitor if it were present. All the allopatric populations evolve to have a similar array of forms. Where both species are present (in sympatry), each species evolves to exploit the resources that it is better adapted to. Competition forces each species to become more specialized. Character displacement shows how ecological competition results in a discrete array of forms within each species.

It is hard to show that character displacement is caused by competition

However, it takes rigorous research to show conclusively that a result such as Figure 13.7 is really caused by ecological competition. Taper & Case (1992), Losos (2000), and Schluter (2000) discuss six criteria that a full study would need to satisfy. For instance,

Figure 13.7

Character displacement in North American salamanders. (a) Character displacement can only be studied in two species with partly overlapping ranges, such that in some places both species are present (sympatry) and in other places only one species is present (allopatry). (b) Where only one of the species of *Plethodon cinereus* or *P. hoffmani* is found (allopatric populations) the form of the species is similar. Where both species are found together (sympatric populations) they differ more. (c) Measurements were made of the skull form, which is related to diet. Redrawn, by permission of the publisher, from Adams & Rohlf (2000).



the pattern could be caused by differences in resources, for example if the insect prey differed between sites, or it could be caused by chance. Adams & Rohlf (2000) came close to ruling out all the alternatives to competition: they met five of the six criteria in their study of the salamanders *P. hoffmani* and *P. cinereus*. These salamanders are about the best example we have of character displacement, and its explanation by ecological competition.

13.7 Some controversial issues exist between the phenetic, biological, and ecological species concepts

We saw in Section 13.2 that the phenetic, ecological and biological species concepts are closely related. Most species probably exist in a phenetic, ecological, and biological

(that is, interbreeding) sense. However, the three factors do not exactly coincide in nature. The cases in which they do not can be used as test cases, to test whether one species concept is superior to another. The controversies have mainly been between the phenetic and the biological species concepts, or between the ecological and the biological species concepts.

13.7.1 *The phenetic species concept suffers from serious theoretical defects*

The phenetic species concept is ambiguous in theory

The phenetic species concept defines a species as a certain set, or cluster, of phenotypic forms. But why should one set of phenotypic forms rather than another be recognized as a species? The classic version of the phenetic species concept was the typological species concept. It defined a species by reference to the “type” of the species. The trouble with this idea is that, as we saw in Section 13.5, types do not exist in Darwinian theory. Typological theories of species are mainly rejected. A more modern version of the phenetic species concept was developed by the numerical taxonomists. They tried to define species simply as phenetic clusters. The trouble with this (as discussed in Section 16.5, p. 476) is that several statistical methods exist for recognizing phenetic clusters, and those methods can disagree about what the clusters are. The definition of species then requires an arbitrary choice between the different statistical procedures. The underlying problem is that distinct phenetic species do not simply exist “out there” in nature. Some species form obvious phenetic units, but others do not and then we need some other criterion to fall back on.

Sibling species are phenetically almost identical

But the criteria that the phenetic concept might fall back on are unable to save the phenetic species concept as a general stand-alone species concept. The phenetic concept might, for example, fall back on the biological species concept, which defines a species as a set of interbreeding organisms. A set of interbreeding organisms often forms a phenetic cluster, but it does not always. If a set of interbreeding organisms always evolved to differ by x phenetic units from the next such set of interbreeding organisms, we could recognize phenetic species as differing x units from the nearest species. But in fact the two biological species may differ by almost any phenetic amount. *Sibling species* are one case in which phenetic and reproductive units do not coincide. Sibling species are pairs of species that differ reproductively but not morphologically. The classic example is the species pair *Drosophila persimilis* and *D. pseudoobscura*. The two species are separate interbreeding units: if flies from a *persimilis* line are put with flies from a *pseudoobscura* line, they do not interbreed. But they are phenetically almost indistinguishable. Sibling species are an extreme example, to illustrate the general point that phenetic and interbreeding units are not the same in nature. Far from saving the phenetic species concept by providing a measure of phenetic distinctness, the biological species concept shows that the phenetic species concept is trying to do something impossible. Phenetic clusters alone do not satisfactorily divide all of life up into species.

The same point can be illustrated by examples at the opposite extreme: a single species (in the biological sense) that contains a huge array of distinct phenetic forms. Some highly “polytypic” species contain many forms, each of which would be distinct enough to count as a separate species on the classic typological definition of a species.

Polytypic species have diverse phenetic forms within one species

Some butterfly species, such as *Heliconius erato* (Section 8.3, p. 197), contain a number of forms that differ more than do most butterfly species. But the forms can interbreed and are all included in the same species. Species like *H. erato* are called “polytypic”: they cannot be defined by reference to one type specimen because they have many distinct forms. Taxonomic practice in sibling species and highly polytypic species follows the biological species concept where sibling species are split into pairs of formally named species, and the many forms of a species such as *H. erato* are all formally named as one species. Many, perhaps most, species form phenetic clusters. But not all do and the phenetic procedures for defining species can only be justified by falling back on the biological species concept. That ultimate reliance on the biological species concept is made clear in difficult test cases such as sibling and highly polytypic species.

13.7.2 *Ecological adaptation and gene flow can provide complementary, or in some cases competing, theories of the integrity of species*

The reproductive and ecological aspects of species are probably usually correlated in nature. Interbreeding among the members of a species results in a set of organisms with shared adaptations to an ecological niche, as we saw in Section 13.2.2. The ecological and biological species concepts are therefore usually not in conflict. However, there are some test cases in which the two concepts make different predictions. For instance, gene flow (migration) can rapidly unify the gene frequencies of separate populations if selection is weak (Section 5.14.4, p. 132). On the other hand, a strong selection force can in theory keep two populations distinct despite gene flow. The relative importance of adaptation to the local ecological conditions and gene flow is an empirical question in cases where the two forces conflict.

Selection can produce divergence despite gene flow

Metal-tolerant grasses show spatial divergence . . .

Bradshaw (1971) carried out a major ecological genetic study of plants, particularly the grass *Agrostis tenuis*, on and around spoil-tips in the UK. Spoil-tips are deposited from metal mining and contain high concentrations of such poisonous heavy metals as copper, zinc, or lead. Only a few plants have been able to colonize them, and of these the grass *A. tenuis* has been studied most closely. It has colonized these areas by means of genetic variants that are able to grow where the concentration of heavy metals is high; around a spoil-tip, therefore, there is one class of genotypes growing on the tip itself, and another class in the surrounding area. Natural selection works strongly against the seeds of the surrounding forms when they land on the spoil-tip: the seeds are poisoned. Selection also acts against the metal-tolerant forms off the spoil-tips. The reason is less clear, but the detoxification mechanism may cost something to possess. Where the mechanism is not needed the grass is better off without it.

Populations of *A. tenuis* show divergence, in that there are markedly different frequencies of genes for metal tolerance on and off the spoil-tips. The pattern is clearly favored by natural selection — but what about gene flow? The biological species concept predicts that gene flow will be low, otherwise the divergence could not have taken

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... despite gene flow

place. In fact, gene flow is large. Pollen blows in clouds over the edges of the spoil-tips and interbreeding between the genotypes is extensive. In this case, selection has been strong enough to overcome gene flow.

The situation in *A. tenuis* fits better with the ecological species concept than the biological species concept. Ecological adaptation, not reduced gene flow, explains the divergence between the grass on and off the spoil-tips. However, the conditions on the spoil-tips are exceptional and recently established. The selective conditions may soon be removed, for instance if the spoil-tips are cleaned up. If the selective conditions do persist, the conflict between gene flow and ecological adaptation may disappear over time. The grass might evolve a flexible genotype that could switch a metal-tolerating mechanism on or off, depending on where the grass grew up. Or a cost-free detoxification mechanism might evolve (in much the same way as pesticide resistance has evolved in insect pests, see Section 10.7.3, p. 276). Alternatively, gene flow may be reduced. The flowering times of the tolerant and normal types already differ in *A. tenuis*, and that will reduce the gene flow between them. In the future the two forms could evolve into two separate species. One way or another, the conflict between gene flow and selection will be short lived. Either the gene flow pattern, or the selection regime, will change. *A. tenuis* is a partial exception to the rule that biological and ecological species concepts usually agree, but the exception is likely to be minor and short lived relative to evolutionary time.

Selection can produce uniformity in the absence of gene flow

Snails show genetic uniformity in the absence of gene flow

In other cases, different populations of a species have similar gene frequencies even though no gene flow seems to occur between the populations. For instance, Ochman *et al.* (1983) studied the snail *Cepaea nemoralis* in the Spanish Pyrenees. The snail rarely lives above 4,600 feet (1,400 m) in the mountains, and never above 6,500 feet (2,000 m) because of the cold. In the Pyrenees, it lives in neighboring river valleys separated by mountains: where those mountains are higher than 4,600 feet (1,400 m), gene flow between valleys will be absent — and there is probably little gene flow even between the valleys in lower mountains. If gene flow is required to maintain the integrity of the species (that is, the similarity of gene frequencies), populations in different valleys should have diverged.

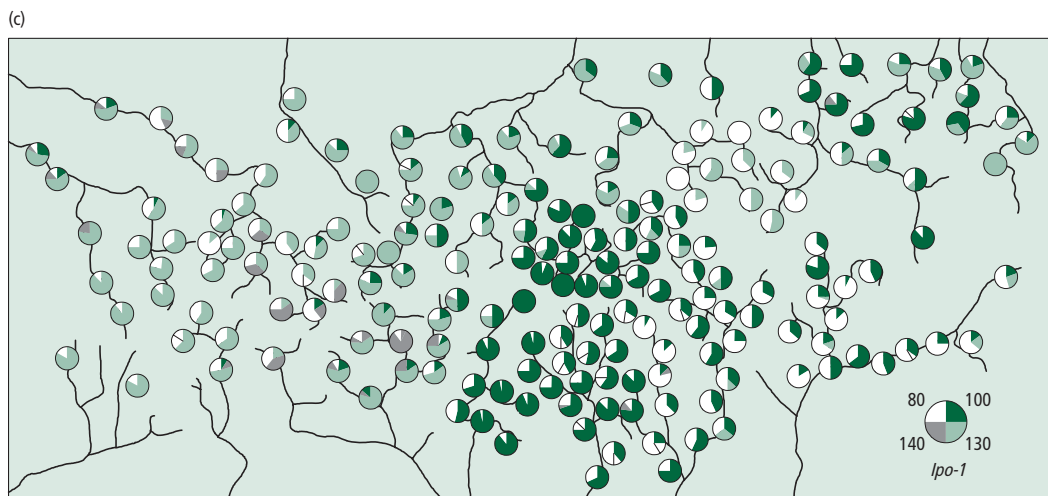
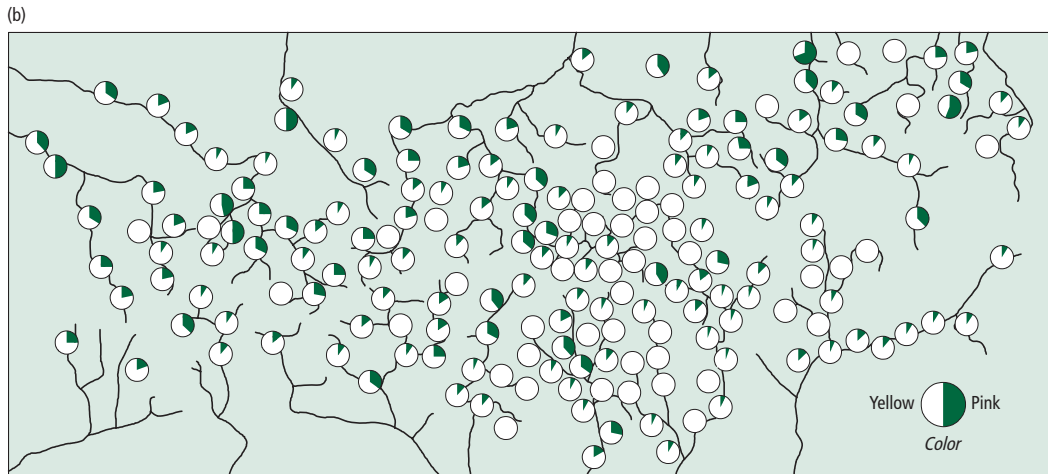
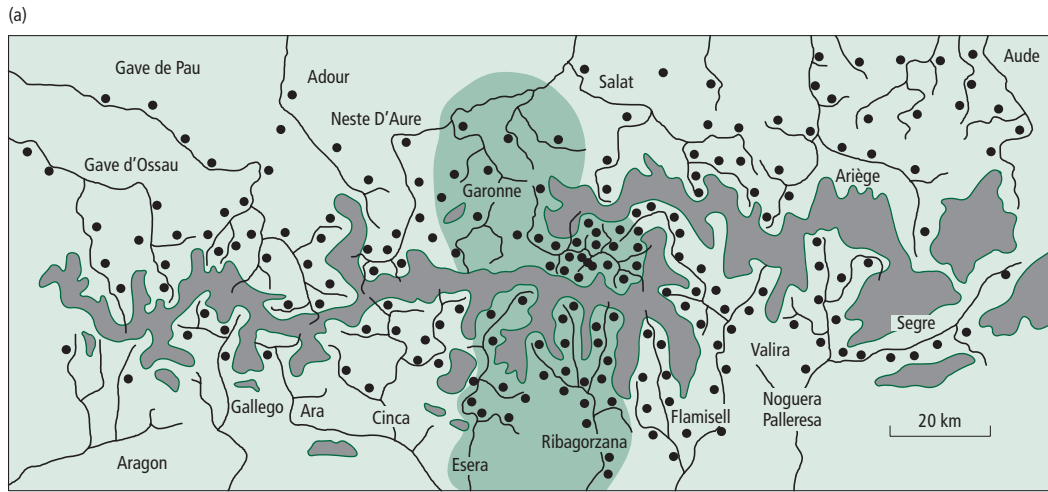
Ochman *et al.* (1983) measured several characters, including the frequencies of four alleles of the gene coding for an enzyme, indophenol oxidase (*Ipo-1*), in 197 populations (shown as dots in Figure 13.8a). As Figure 13.8c shows, the *Ipo-1* alleles

Figure 13.8 (opposite)

(a) Map of the Pyrenees showing sites where the snail *Cepaea nemoralis* was sampled and the river valleys. The rivers are separated by high ground and mountains, and the shaded gray area running from left to right indicates regions where the altitude exceeds 4,900 feet (1,500 m). The stippled green area in the middle indicates the area around which gene frequencies are differentiated: see (c) below. (b) Shell morphology (in this case, background color) shows little geographic variation.

(c) Protein polymorphism, however, falls into three main areas. The map is for the four alleles of one enzyme, indophenol oxidase (*Ipo-1*). Three or so regions can be seen from left to right, with characteristic gene frequencies: to the left, allele 130 is more frequent, in the center, allele 100 is more frequent, and to the right allele 80 is more frequent. These regions transcend the high grounds shown in (a). Similarity within an area is unlikely to be maintained by gene flow. Redrawn, by permission of the publisher, from Ochman *et al.* (1983).

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divide the snails into three main regions. From the left, the first main region has a relatively high frequency of allele 130; the second has a high frequency of allele 100; and the right-hand region has a higher frequency of allele 80. These regions transcend the mountain barrier to gene flow, which is shown as a gray region from left to right in Figure 13.8a. The similarity of the populations within each of the three regions, on both sides of a barrier to gene flow, is difficult to explain by the biological species concept. The ecological species concept might be able to explain the pattern, but we need further research on how the different alleles are adapted to different regions across the map.

Asexual forms . . .

A further test case comes from asexual species. The ecological species concept predicts equally clear-cut species in both sexual and asexual forms. There is no reason why only sexual, and not asexual, forms should inhabit niches, and selection should therefore maintain asexual species in integrated clusters much like sexual species. But the biological species concept predicts a difference. Asexual forms do not interbreed and no gene flow occurs. If gene flow holds species together, then asexual forms should have blurred edges; nothing will stop asexual species from blurring into a continuum. Sexual forms should be more clearly discrete than their asexual relatives.

. . . may . . .

Unfortunately, the evidence published so far is indecisive. On the one hand, many authors — especially critics of the biological species concept, Simpson (1961b) being an example — have asserted that asexual species form integrated phenetic clusters just like sexual species. This is supported by the study of Holman (1987) on rotifers. Bdelloid rotifers are a large asexual taxon (Section 12.1.4, p. 319). The monogont rotifers are the sister taxon of the bdelloids, but monogonts are at least sometimes sexual. Holman showed that species in bdelloids have been recognized at least as consistently as in monogonts.

. . . or may not . . .

On the other hand, examples also exist of asexual forms that do not form distinct species. Maynard Smith (1986) has pointed to the example of hawkweed (*Hieracium*). It reproduces asexually and is highly variable, such that taxonomists have recognized many hundreds of “species,” and no two taxonomists agree on how many forms there are. In all, asexual species are a potentially interesting test case, but the evidence that has so far been assembled does not point to a definite conclusion.

. . . exist as distinct species

Bacteria, and other microbes, illustrate much the same point. Bacteria mainly reproduce asexually, and yet distinct species of bacteria are named just like in multicellular, sexual life forms. This could mean that the biological species concept is inadequate because it is unable to account for bacterial species. However, genetic exchange does take place between bacterial cells. The units recognized as species in bacteria may then be maintained by gene flow. Alternatively, bacteria may not really form distinct species, and the habit of naming bacterial “species” may be misleading. The evidence about genetic variation in bacteria is too limited to allow a broad conclusion about bacteria as a whole. Much is known about the population genetics of a few bacteria, such as *Escherichia coli*, but the population genetics of most microbes remains obscure. One popular interim conclusion is that some bacteria have extensive genetic exchange between cells and form good species, but other bacteria have little genetic exchange and the application of species concepts in them may be problematic. Cohen (2001) and Lan & Reeves (2001) discuss microbial species. Maynard Smith *et al.* (1993) look at the kind of data that are needed. Meanwhile bacteria, like asexual forms generally, pose a

Microbes show clearer species in some cases than in others

problem for the future, rather than contributing decisive evidence in the present, for the controversies about biological species.

13.7.3 *Both selection and genetic incompatibility provide explanations of reduced hybrid fitness*

Ecological factors can influence the fitness of hybrids

When closely related species can produce hybrids, the hybrid offspring often have low fitness. The hybrids may be sterile (for example, mules) or have reduced viability. The reduced fitness of the hybrids is an example of postzygotic isolation (see Table 13.1), and may be explained by either or both of two processes. One is that the hybrids may have a form that is intermediate between the two parental species and be maladapted because few resources exist for an intermediate form. In an area where seeds are large or small, one species may have large beaks and another species have small beaks. Hybrids between the two species may have low fitness because few medium-sized seeds are available. This is an ecological theory of low hybrid fitness. It can be illustrated by a study of Darwin's finches by Grant & Grant (2002).

The medium ground finch *Geospiza fortis* lives on the island of Daphne Major, in the Galápagos, and it eats relatively large, hard seeds. The small ground finch *G. fuliginosa* is an occasional immigrant. It eats smaller seeds, and has a lower survival rate than *G. fortis* in normal conditions, when the supply of small seeds is low. The immigrant *G. fuliginosa* hybridizes with the resident *G. fortis*, producing hybrids with intermediate-sized beaks. The hybrids also mainly eat small seeds, and have relatively low survival in normal conditions (Table 13.2). But following the El Niño event, the supply of small seeds increased massively (see Section 9.1, p. 223, and Plate 4, between pp. 68 and 69). The fitness of the hybrids now increased, to at least as high a level as *G. fortis*. The degree of postzygotic isolation between *G. fortis* and *G. fuliginosa* depends on the food supply.

Table 13.2

Hybrid fitness (and therefore postzygotic isolation) between two species of Darwin's finches depends on the food supply. In normal years, small seeds are rare and pure *Geospiza fortis* individuals have higher fitness; following El Niño, the supply of small seeds increases and hybrid fitness improves. Fitness is here measured by survival from egg to first year. (Other measures of fitness showed the same trend.) From Schluter (2000), from data of Grant & Grant.

	Survival to first year
Normal years	
<i>fortis</i> × <i>fuliginosa</i> hybrids	0.16
<i>fortis</i> × <i>fortis</i>	0.32
El Niño year	
<i>fortis</i> × <i>fuliginosa</i> hybrids	0.84
<i>fortis</i> × <i>fortis</i>	0.82

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Low hybrid fitness may also be due to genetic incompatibilities

Most of the time, small seeds are rare and the hybrids have low fitness. The Grants' measurements show that the reason for the low fitness is that they are poorly adapted ecologically.

Alternatively, hybrids may have low fitness because the two parental species contain genes that do not work well when put together in a hybrid offspring. Section 14.4 (p. 389) will look at this theory further. Suppose that one member of species 1 contains genes *A* and *B* at two loci, and members of species 2 contain genes *a* and *b*. *A* and *B* work well together and produce a good, functioning body, as do genes *a* and *b*. But a hybrid may contain genes *A* and *b*. These two genes may be incompatible. (A crude example would be for *A* and *B* to code for a long left and right leg, and *a* and *b* for a short left and right leg. The unfortunate hybrids would then have one long and one short leg.) This is a genetic explanation for low hybrid fitness. The mule (a hybrid between a male ass *Equus africanus* and a female horse *E. caballus*) is probably explained by some incompatibility between the genes of asses and horses.

Ecological maladaptation and genetic mismatches can be competing hypotheses to explain any one case of low hybrid fitness. They can be tested between, but the conflict should not be exaggerated. Both factors probably operate in nature, and both can be incorporated into our understanding of species. For instance, the ecological explanation of low hybrid fitness may apply more to closely related species living in the same area. They may hybridize sufficiently often for their genes to remain compatible. Such may be the case in Darwin's finches. The genetic explanation may become more important over time, as two species diverge and their genes become increasingly different.

Ecological and reproductive factors are likely both at work

In summary, nature has supplied us with certain test cases to examine the processes invoked by the biological and ecological species concepts. The processes (ecological adaptation and gene flow) probably usually act together to produce the same result. In some cases, the two processes appear to be in conflict. The test cases may be short lived (as in *Agrostis tenuis*) and of little evolutionary importance; or the results may be ambiguous (as in asexual species); or the test cases may suggest that both processes should be incorporated in the two concepts (as in the theories of low hybrid fitness). The evidence seems to suggest that both ecological adaptation and interbreeding are needed to explain the sets of forms that we recognize as species. Some biologists, therefore, have suggested that we need a more general species concept. Templeton (1998), for instance, favours a "cohesion species concept," in which all species show "cohesion" (that is, species exist as discrete phenetic clusters) but the reason may differ from one species to another. Some species may exist because of ecological adaptation, others because of gene flow, others because of a mix of the two.



13.8 Taxonomic concepts may be nominalist or realist

13.8.1 *The species category*

When we classify the natural world into units such as species, genera, and families, are we imposing categories of our own devising on a seamless natural continuum, or are the categories real divisions in nature? The problem is an old one. It applies to all

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Biological species are real, not nominal units

taxonomic categories, but has particularly been discussed in the case of the species category. The idea that species are artificial divisions of a natural continuum is called *nominalism*; the alternative, that nature is itself divided into discrete species, is called *realism*.

On the biological species concept, species are real rather than nominal units in nature. If we take the set of all organisms currently classified as human beings and as chimpanzees, then these organisms do divide into two discrete reproductive units. A human being can interbreed with any other human (subject to provisos, such as that the two humans are of opposite sex and of reproductive age), but with no chimpanzee. Interbreeding between species does not blur out. Here is a thought experiment to illustrate what “blurring out” would mean. Take the set of all human plus all chimpanzee individuals. Then pick an individual at random. Now experimentally place that individual with a range of potential mates from across the entire set of other individuals. If reproductive output varied continuously from 100% to 0% across the full set of mates, then interbreeding could be said to blur out. In fact reproductive output would jump between 100% (or a high figure) and 0% with nothing in between. Human and chimpanzee interbreeding does not blur out. In a way, the strangeness of imagining what blurring out would mean illustrates how humans and chimpanzees form real, not nominal, reproductive units. In any case, humans in fact form a real reproductive unit. So too do most species.

Species are likely to form phenetic units in consequence. Because interbreeding is confined to a certain set of individuals, an advantageous new mutation will spread through that set of individuals, but not into other such sets (that is, other species). If chimpanzees gain a favorable mutation, it will not spread to us even if we would benefit from it. For this reason, biological species often form real, rather than nominal, phenetic clusters. The most striking evidence that species exist as phenetic clusters comes from “folk taxonomy.” People working independently of Western taxonomists usually have names for the species living in their area, and we can look at whether they have hit on the same division of nature into species as have Western taxonomists working with the same raw material. Some people, it seems, do use much the same classification of species. The Kalám of New Guinea, for instance, recognize 174 vertebrate species, all but four of which correspond to species recognized by Western taxonomists.

Folk taxonomy often matches formal taxonomy

As we saw (Section 13.7.1), phenetic and reproductive units do not always coincide. In polytypic butterfly species, there are many discrete phenetic forms and “folk taxonomies” of these butterflies tend to recognize many forms rather than the single biological species. Likewise, folk taxonomies would probably not distinguish sibling species, though most sibling species are too obscure for this question even to have been asked. In summary, species in nature are real rather than nominal interbreeding units in most cases, but not in all.

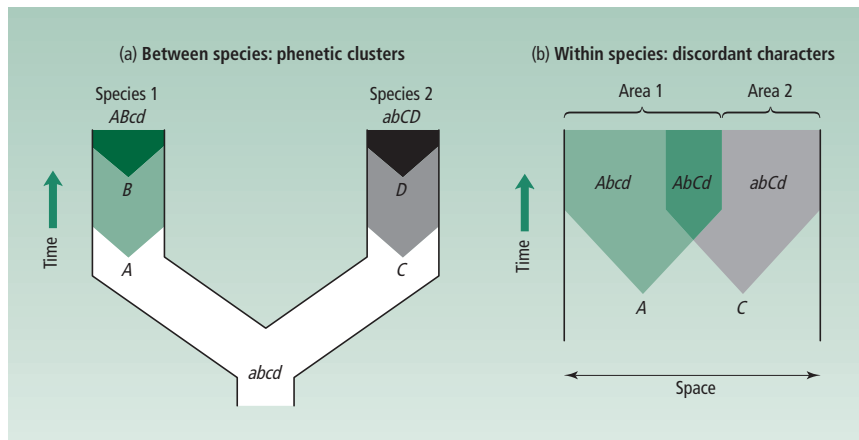
13.8.2 *Categories below the species level*

Species in many cases form discrete phenetic units. This contrasts with subspecific units such as “subspecies” and “races.” (I put the words in quotes because, although the categories are sometimes used, biologists are skeptical about their utility for the reason we are about to look at.) Subspecies and races — the two terms are almost

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Figure 13.9

Different species form relatively discrete genetic (and usually phenetic) units; different subspecific units such as races do not. (a) Evolution in two species. Successive genes spread within each species. Species 1 forms a cluster with genes *A* and *B*; species 2 is a distinct cluster with genes *C* and *D*. No individuals have a discordant gene combination such as *AbcD*. (b) Evolution within one species. Advantageous and neutral genes spread locally. Different genes may spread in different places, partly depending on the local conditions. Discordant gene combinations can easily arise, and in area 1 some individuals have the gene (*C*) found in area 2 and other individuals do not. To produce discordant gene combinations between species, a gene (such as *C*) would need to spread not only through species 2 but also through part of species 1. This is usually impossible because of isolating barriers between species. The argument here applies to phenetic characters as well as genes, in so far as the genes code for distinct phenetic characters.



interchangeable — are defined as geographic populations within a species that have a distinct phenetic appearance. The trouble is that variation within a species does not form discrete genetic phenetic clusters in the way that differences between species often do. Sparrows in North America, for example, form a cline in body size from south to north (see Figure 13.5). Northern sparrows are bigger, because of adaptation to temperature. But if we looked at a second character, such as their vocalizations (song) or the frequency of a gene, there is no reason to expect it to form a cline along the same gradient. It might form a complicated gradient related to the rainfall or another factor. Different characters form different spatial patterns, related to different adaptive factors or random drift.

Thus the distributions of different characters within a species are “discordant.” Nothing forces the sparrows in one area to form a discrete genetic or phenetic cluster. Interbreeding and non-interbreeding cause different species to form phenetic clusters. The distributions of different characters tend to be concordant, as one mutation after another is fixed within a species (Figure 13.9). Within a species, any character distribution is possible. This is part of the reason why discrete races cannot be recognized in the human species. (The problem is compounded by the low genetic variation within our species; see Box 13.2.) When different people have tried to classify human races, they have found as few as six or as many as 60 races. An objective classification is impossible because different characters vary independently within a species. Skin color, eye shape, and blood groups form independent and discordant clines. This does not show that race is a meaningless concept for human beings. It has cultural and political meanings, but race has a nominal rather than a real meaning in evolutionary biology.

13.8.3 Categories above the species level

The reality of taxonomic categories above the species level in part depends on how those categories are defined, and that is a later topic (Chapter 16). However, one point

Biologists disagree about how real the higher taxonomic units are

can be made here. Evolutionary biologists who support the biological species concept characteristically differ from those who support the ecological species concept in their attitude to the reality of taxa above the species level. The biological species concept can apply to only one taxonomic level. If species are defined by interbreeding, then genera, families, and orders must exist for some other reason. Mayr has been a strong supporter of the biological species concept and (in 1942, for example) duly reasoned that species are real, but that higher levels are defined more phenetically and have less reality; that is higher levels are relatively nominalistic. Dobzhansky and Huxley held a similar position.

Simpson, however, favored a more ecological theory of species. The ecological concept can apply in much the same way at all taxonomic levels. If the lion occupies an adaptive zone corresponding to a single ecological niche, then the genus *Felis* may occupy a broader adaptive zone, and the class Mammalia an even broader adaptive zone. Adaptive zones could have a hierarchical pattern corresponding to (and causing) the taxonomic hierarchy. All taxonomic levels could then be real in the same way. The relative reality of the species, and of higher taxonomic levels, is therefore part of the larger controversy between the ecological and reproductive species concepts.

13.9 Conclusion

In evolutionary biology, the interesting questions about species are theoretical. The practical question of which actual individuals should be classified into which species can on occasion be awkward, but biologists do not tie themselves in knots about it. The majority — perhaps over 99.9% of specimens can be fitted into conventionally recognized species and do not raise even practical problems. Other specimens can be identified after a bit of work — or even left on one side until more is learned about them.

The more interesting question is why variation comes in nature arranged in the clusters we recognize as species. There are several possible answers, as we have seen. Different species concepts follow from different ideas about the importance of interbreeding (or gene flow) and natural selection. It is sometimes possible to test between them, but the results so far have not been enough to confirm any one concept (or any plurality of concepts) decisively. However, there is general agreement that phenetic distinction alone is not an adequate concept, and that the key explanatory processes are interbreeding and the pattern of ecological resources.

Summary

- 1** In practice, species are defined by easily recognizable phenetic characters that reliably indicate what species an individual belongs to.
- 2** The biological species concept defines a species as a set of interbreeding forms. Interbreeding between species is prevented by isolating mechanisms.
- 3** The ecological species concept defines a species as a set of organisms adapted to a particular ecological niche.
- 4** The phenetic species concept defines a species as a set of organisms that are sufficiently phenetically similar to one another.
- 5** The biological, ecological, and phenetic (and several other) species concepts are all closely related, and are concerned to explain or describe much the same fact: that life seems to come in the form of distinct species.
- 6** Individuals mainly interbreed with other members of their own species because of isolating barriers that prevent interbreeding with other species. Isolating barriers can be prezygotic or postzygotic.
- 7** Geographic variation can be adaptive or neutral. The amount of genetic variation among geographic races of a species can be described quantitatively and is low in human beings relative to other species.
- 8** The theory of evolution justifies population thinking rather than typological thinking about intra-specific variation: all individuals in a population are equally good members of a species, rather than some being better specimens than others.
- 9** Character displacement occurs when two species have partly overlapping geographic ranges and the two species differ more in sympatry than in allopatry. Character displacement maybe caused by ecological competition.
- 10** The biological species concept explains the integrity of species by interbreeding (which produces gene flow), the ecological concept by selection. The two processes are usually correlated, but it is possible to test between them in special cases. Selection can be strong enough to overcome gene flow, and selection can maintain a species' integrity in the absence of gene flow.
- 11** Taxonomic entities such as biological species may be real or nominal. According to the biological species concept, species can be real, but lower and higher taxonomic levels are nominal. According to the ecological species concept, all taxonomic levels can have a similar degree of realism.

Further reading

Mayr (1963) is the classic account of the species in evolutionary biology; see also Mayr (1976, 2001) and Mayr & Ashlock (1991). Coyne (1994) discusses species concepts, particularly in relation to Mayr's ideas. Dobzhansky (1970), Huxley (1942), Cain (1954), and Simpson (1961b) also contain classic material. Ereshefsky's (1992) anthology contains many of the important papers on species concepts.

More recent books include the volume edited by Howard & Berlocher (1998), which has good chapters on species concepts by Harrison, Templeton, Shaw, and de Queiroz that discuss the use of molecular markers and coalescence. See Levin (2000) on plants. Two other recent books are by Hey (2001) and by Ereshefsky (2001), both of whom

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question whether species, as recognized in conventional Linnaean classification, correspond to species as fundamental evolutionary units. The practical problems of species definition are dealt with in most general books about classification, which I list in the further reading for Chapter 16.

On the biological species concept, see almost every source in the previous paragraphs, particularly those by Mayr. On the ecological concept, see Van Valen (1976). On the phenetic species concept, see Sneath & Sokal (1973) and many of the references in Chapter 16. Paterson (1993) is the main source for the recognition species concept, as well as the authors in Lambert & Spencer (1994). For criticism, see Coyne *et al.* (1989). Ritchie & Phillips (1998) provide evidence of intraspecific variation in SMRS, in contrast with the theory that stabilizing selection acts on SMRS. See also the material on antagonistic sexual selection in Section 12.4.7 of this text.

For isolating mechanisms see the books by Mayr and Dobzhansky above. On plants, see Grant (1981) and Levin (2000). For background on the African cichlids, see Stiassny & Meyer (1999). See also Fryer (2001).

For geographic variation the classic source is again Mayr (1963), and the topic is covered in population genetic texts such as those listed in Chapter 5 in this book. For more on the *Linanthus* example, see Wright (1978) for background and Turelli *et al.* (2001b) for the cutting edge of modern research. Huey *et al.* (2000) is a nice example of recently evolved geographic variation. On population versus typological thinking, see Ghiselin (1997) and Hull (1988) in addition to Mayr (1976 — of which I extracted one classic essay in Ridley (1997)). Pre-Darwinian taxonomists have, since Mayr, often been criticized as typologists. However, the distinction between population and typological thinking is better used conceptually than historically — Winsor (2003) argues that essentially no pre-Darwinian taxonomists were typologists, though they did not appreciate variation in the way we now do.

Character displacement is well reviewed by Schluter (2000), most recently, and by Taper & Case (1992). Brown & Wilson (1958) is the original source. Schluter (2000, pp. 166–8) has a table of other examples such as the salamanders, together with information on how well they have been studied. Another classic example comes from Darwin's finches, and chapter 10 of Weiner (1994) is a popular account, while Grant (1986) contains a more authoritative discussion of it.

The difficulties in the phenetic species concepts are a special case of the difficulties in all phenetic classification: see the references in Chapter 16 later in this book. On heavy metal tolerance in plants, see Bradshaw (1971) and Ford (1975), and Palumbi (2001b) on human-driven evolution in general.

European oaks are a further good case study in ecological versus biological (gene flow) species concepts: see Van Valen (1976) again, and Muir *et al.* (2000). Other recent studies of selection and gene flow include Blondel *et al.* (1999) on blue tits in Corsica, and Smith *et al.* (1997) on rainforest biodiversity. The ecological and genetic explanations of hybrid fitness are discussed in Schluter (2000) and many of the papers about reinforcement, hybrid speciation in plants, and the Dobzhansky–Muller theory that are referred to in Chapter 14.

Berlin (1992) is a book about folk taxonomy, and Gould (1980) contains a popular essay on the subject.

Study and review questions

- 1 Review the main arguments for and against the phenetic, biological, and ecological species concepts.
- 2 In a pair of "sibling species," how many species are there in the: (i) phenetic, (ii) biological, and (iii) ecological species concepts?
- 3 Review the kinds of prezygotic and postzygotic isolating barriers that exist.
- 4 Calculate the statistic G_{ST} , which describes the amount of geographic differentiation within a species, for species 1–3 below.

Species	H_T	H_S	G_{ST}
1	0.5	0.5	
2	0.5	0.25	
3	0	0	

What biological factors might cause G_{ST} to be lower in some species than in others?

- 5 Do asexual organisms form species like sexual organisms, and what consequences does the answer have for our concept of species?
- 6 Is population or typological thinking more appropriate in classifying the following entities? (The answer is not certain in all cases, and they are as much topics to think about and discuss, as to provide final answers about.) (i) Chemical elements (such as atoms of carbon, hydrogen, gold, etc.); (ii) human cultures; (iii) biological species; (iv) human emotions (such as fear, anger, etc.); (v) mechanisms of transport (such as cars, walking, airplanes, and so on); and (vi) scientific theories (such as evolution, gravity, quantum theory, etc.).
- 7 How can we test between the ecological and genetic theories of postzygotic isolation?
- 8 In the (i) phenetic, (ii) biological, and (iii) ecological species concepts, are (a) species, (b) subspecies/races, and (c) higher taxonomic categories, real or nominal entities in nature?