

Darwin had no evidence for his position; it means that his argument was more complex than might first appear.

Matters are much more straightforward now. Modern biologists have observed speciation events. Indeed, they have even caused them. As will be discussed in Chapter 6, one standard (though not uncontroversial) idea about species is that they are reproductively isolated from each other. Two contemporary populations are said to belong to different species if they cannot produce viable fertile offspring with each other. Botanists have found that the chemical *colchicine* causes *ploidy*—a modification in the number of chromosomes found in an organism. For example, by administering colchicine, a botanist can produce tetraploid plants that are reproductively isolated from their diploid parents. The daughter and parent populations satisfy the requirement of reproductive isolation. We now have *observational* evidence that species boundaries are not cast in stone.

In summary, Darwin advanced a claim about pattern and a claim about process. The pattern claim was that all terrestrial organisms are related genealogically; life forms a tree in which all contemporary species have a common ancestor if we go back far enough in time. The process claim was that natural selection is the principal cause of the diversity we observe among life forms. However, neither of these claims was the straightforward report of what Darwin *saw*. This raises the question of how a scientist can muster evidence for hypotheses that go beyond what is observed directly. I'll address this problem in Chapter 2.

1.4 Historical Particulars and General Laws

Some sciences try to discover general laws; others aim to uncover particular sequences of historical events. It isn't that the "hard" sciences only do the former and the "soft" sciences strive solely for the latter. Each broad discipline contains subareas that differ in how they emphasize one task or the other.

Within physics, compare the different research problems that a particle physicist and an astronomer might investigate. The particle physicist might seek to identify general principles that govern a certain sort of particle collision. The laws to be stated describe what the outcome of such a collision would be, no matter *where* and no matter *when* it takes place. It is characteristic of our conception of laws that they should be *universal*; they are not limited to particular regions of space and time.

Laws take the form of if/then statements. Isaac Newton's universal law of gravitation says that the gravitational attraction between any two objects is directly proportional to the product of their masses and inversely proportional to the square of the distance between them. The law does not say that the universe contains two, four, or any number of objects. It just says what would be true *if* the universe contained objects with mass.

In contrast, astronomers typically will be interested in obtaining information about a unique object. Focusing on a distant star, they might attempt to infer its temperature,

density, and size. Statements that provide information of this sort are not if/then in form. Such statements describe historical particulars and do not state laws.

This division between *nomothetic* (“nomos” is Greek for *law*) and *historical sciences* does not mean that each science is exclusively one or the other. The particle physicist might find that the collisions of interest often occur on the surface of the sun; if so, a detailed study of that particular object might help to infer the general law. Symmetrically, the astronomer interested in obtaining an accurate description of the star might use various laws to help make the inference.

Although the particle physicist and the astronomer may attend to both general laws and historical particulars, we can separate their two enterprises by distinguishing *means* from *ends*. The astronomer’s problem is a historical one because the goal is to infer the properties of a particular object; the astronomer uses laws only as a means. Particle physics, on the other hand, is a nomothetic discipline because the goal is to infer general laws; descriptions of particular objects are relevant only as a means.

The same division exists within evolutionary biology. When a systematist infers that human beings are more closely related to chimps than they are to gorillas, this phylogenetic proposition describes a family tree that connects three species. The proposition is logically of the same type as the proposition that says that Alice is more closely related to Betty than she is to Carl. Of course, the family tree pertaining to species connects *bigger* objects than the family tree that connects individual organisms. But this difference merely concerns the size of the objects in the tree, not the basic type of proposition that is involved. Reconstructing genealogical relationships is the goal of a *historical science*.

The same can be said of much of paleobiology. Examining fossils allows the biologist to infer that various mass extinctions have taken place. Paleobiologists identify which species lived through these events and which did not. They try to explain why the mass extinctions took place. Why did some species survive while others did not? In similar fashion, a historian of our own species might try to explain the mass death of South American Indians following the Spanish Conquest. Once again, the units described differ in size. The paleobiologist focuses on whole species; a historian of the human past describes individual human beings and local populations.

Phylogenetic reconstruction and paleobiology concern the distant past. But historical sciences, as I am using that term, often aim to characterize objects that exist in the present as well. A field naturalist may track gene or phenotypic frequencies in a particular population. This is what Kettlewell (1973) did in his investigation of industrial melanism in the peppered moth (*Biston betularia*). The project was to describe and explain a set of changes. Field naturalists usually wish to characterize particular objects, not to infer general laws.

Are there general laws in evolutionary biology? Although some philosophers (Smart 1963; Beatty 1981) have said no, I want to point out that there are many interesting if/then generalizations afoot in evolutionary theory.

Biologists usually don't call them "laws"; "model" is the preferred term. When biologists specify a model of a given kind of process, they describe the rules by which a system of a given kind changes. Models have the characteristic if/then format that we associate with scientific laws. These mathematical formalisms say what will happen *if* a certain set of conditions is satisfied by a system. They do not say *when* or *where* or *how often* those conditions are satisfied in nature.

Consider an example. R. A. Fisher (1930), one of the founders of population genetics, described a set of assumptions that entails that the sex ratio in a population should evolve to 1:1 and stay there. Mating must be at random, and parental pairs must differ in the mix of sons and daughters they produce (and this difference must be heritable). Fisher was able to show, given his assumptions, that selection will favor parental pairs that produce just the minority sex. For example, if the offspring generation has more males than females, a parental pair does best by producing all daughters. If the population sex ratio is biased in one direction, selection favors traits that reduce that bias. The result is an even mix of males and females.

Fisher's model considers three generations—parents produce offspring who then produce grandoffspring. What mix of sons and daughters should a parent produce if she is to maximize the number of grandoffspring she has? If there are N individuals in the grandoffspring generation, and if the offspring generation contains m males and f females, then the average son has N/m offspring and the average daughter has N/f offspring. A mother thereby gains a benefit of N/m from each of her sons and a benefit of N/f from each of her daughters—these "benefits" being the number of grandoffspring they give her. So individuals in the offspring generation who are in the minority sex on average have more offspring. Hence, the best strategy for a mother is to produce offspring solely of the minority sex. On the other hand, if the sex ratio in the offspring generation is 1:1, a mother cannot do better than the other mothers in the population by having an uneven mix of sons and daughters. A 1:1 sex ratio is a stable equilibrium. A more exact description of Fisher's argument is provided in Box 1.3.

Fisher's elegant model is mathematically correct. If there is life in distant galaxies that satisfies his starting assumptions, then a 1:1 sex ratio must evolve. Like Newton's universal law of gravitation, Fisher's model is not limited in its application to any particular place or time. And just as Fisher's model may have millions of applications, it also may have none at all. The model is an if/then statement; it leaves open the possibility that the *ifs* are never satisfied. Field naturalists have the job of saying whether Fisher's assumptions apply to this or that specific population.

In deciding whether something is a law or a historical hypothesis, one must be clear about which *proposition* one wishes to classify. For example, to ask whether "natural selection" is a law is meaningless until one specifies which proposition about natural selection is at issue. To say that natural selection is responsible for the fact that human beings have opposable thumbs is to state a historical hypothesis; but to say that natural selection will lead to an even sex ratio in the circumstances that

Box 1.3 Fisher's Sex Ratio Argument

The accompanying text provides a simplified rendition of Fisher's argument. In point of fact, Fisher did not conclude that there should be *equal numbers* of males and females but that there should be *equal investment*. A mother has a total package of energy (T) that she can use to produce her mix of sons and daughters. Suppose p is the percentage of energy she allots to sons, that each son costs c_m units of energy to raise, and that a son brings in b_m units of benefit. With a similar representation of the costs and benefits of daughters, a mother's total benefit from her sons and daughters is

$$b_m[pT/c_m] + b_f[(1-p)T/c_f].$$

Suppose all mothers (the "residents") residing in the population allocate p and $(1-p)$ of their resources to sons and daughters, respectively. When will a mother do better by departing from this behavior—i.e., by allotting p^* and $(1-p^*)$ to sons and daughters (where $p \neq p^*$)? This novel mother does better than the other mothers precisely when

$$b_m[p^*T/c_m] + b_f[(1-p^*)T/c_f] > b_m[pT/c_m] + b_f[(1-p)T/c_f],$$

which simplifies to

$$(b_m/c_m - b_f/c_f)(p^* - p) > 0.$$

Recall from the accompanying text that a son provides a benefit of N/m and a daughter provides a benefit of N/f . Substituting these for the benefit terms in the above expression, we obtain

$$(N/mc_m - N/fc_f)(p^* - p) > 0.$$

When the residents invest equally in sons and daughters ($mc_m = fc_f$), no mutant strategy can do better than the resident strategy. And when the residents invest *unequally*, a mutant will do better than the residents by investing exclusively in the sex in which the residents have *underinvested*.

How does investment in the two sexes affect the numbers of sons and daughters produced? In human beings, males have a higher mortality rate, both prenatally and postnatally. This means that the average son costs less than the average daughter. In this case, equal investment entails that an excess of males is produced at birth, which is what we observe.

Fisher's argument assumes that there is random mating in the offspring generation. The import of this assumption was first explored by Hamilton (1967). If there is strict brother/sister mating, then a parent maximizes the number of grandoffspring she has by producing a female-biased sex ratio among her progeny.

Fisher described is to state a law. (Evolutionary laws will be discussed further in Section 3.4.)

Although inferring laws and reconstructing history are distinct scientific goals, they often are fruitfully pursued together. Theoreticians hope their models are not vacuous; they want them to apply to the real world of living organisms. Likewise, naturalists who describe the present and past of particular species often do so with an eye to providing data that have a wider theoretical significance. Nomothetic and historical disciplines in evolutionary biology have much to learn from each other.

An example of a particularly recalcitrant problem in current theory may help make this clear. We presently do not understand why sexual reproduction is as prevalent as it is. The problem is not that theoreticians cannot write models in which sexual reproduction is advantageous. There are lots of such models, each of them mathematically correct. Indeed, there also are many models that show that under specified conditions, sex will be *dis*advantageous.

The difficulty is not that the models are wrong as *if/then* statements but that they often fail to apply to nature. In the real world, some species are sexual, whereas others are not. These different species live under a variety of conditions, and their phylogenetic backgrounds differ as well. What we would like is a model that fits the diversity we observe. To date, no model can claim to do this.

If model building (the pursuit of laws) proceeded independently of natural history, the evolution of sex would not be puzzling. A model can easily show how sex *might* have evolved; *if* the assumptions of the model were satisfied by some natural population, that population would evolve a sexual mode of reproduction. It is a historical question whether this or that population actually satisfied the assumptions in the model. Only by combining laws and history can one say why sex *did* evolve.

1.5 The Causes of Evolution

Although the data of natural history are indispensable to evolutionary model building, there is a place for model building that floats free from the details of what we have observed. Fisher (1930, pp. viii-ix) put the point well when he remarked that “no practical biologist interested in sexual reproduction would be led to work out the detailed consequences experienced by organisms having three or more sexes; yet what else should he do if he wishes to understand why the sexes are, in fact, always two?” We often understand the actual world by locating it in a broader space of possibilities.

Models map out the possible causes of evolution. What are these possible causes? I have already mentioned *natural selection*; heritable variation in fitness can produce evolution. And in Section 1.1, I explained how the *system of mating* in a population can modify the frequencies of different genotypes. There are other possible causes as well.

Gene frequencies can change because of *mutation*. A population that is 100 percent *A* can evolve away from this homogeneous state if *A* genes mutate into *a* genes. A