

Are ecological and evolutionary theories scientific?

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ABSTRACT

Scientists observe nature, search for generalizations, and provide explanations for why the world is as it is. Generalizations are of two kinds. The first are descriptive and inductive, such as Boyle's Law. They are derived from observations and therefore refer to observables (in this case, pressure and volume). The second are often imaginative and form the axioms of a deductive theory, such as Newton's Laws of Motion. They often refer to unobservables (e.g. inertia and gravitation). Biology has many inductive generalizations (e.g. Bergmann's Rule and 'all cells arise from preexisting cells') but few, if any, recognized universal laws and virtually no deductive theory. Many biologists and philosophers of biology have agreed that predictive theory is inappropriate in biology, which is said to be more complex than physics, and that one can have nonpredictive explanations, such as the neo-Darwinian Theory of Evolution by Natural Selection. Other philosophers dismiss nonpredictive, explanatory theories, including evolutionary 'theory', as metaphysics. Most biologists do not think of themselves as philosophers or give much thought to the philosophical basis of their research. Nevertheless, their philosophy shows in the way they do research. The plethora of *ad hoc* (i.e. not universal) hypotheses indicates that biologists are reluctant inductivists in that the search for generalization does not have a high priority. Biologists test their hypotheses by verification. Theoretical physicists, in contrast, are deductive unifiers and test their explanatory hypotheses by falsification.

I argue that *theoretical* biology (concerned with unobservables, such as fitness and natural selection) is not scientific because it lacks universal laws and predictive theory. In order to make this argument, I review the differences between verificationism and falsificationism, induction and deduction, and descriptive and explanatory laws. I show how these differ with a specific example of a successful and still useful (even if now superseded as explanatory) deductive theory, Newton's Theory of Motion. I also review some of the philosophical views expressed on these topics because philosophers seem to be even more divided than biologists, which is not at all helpful.

The fact that biology does not have predictive theories *does not* constitute irrefutable evidence that it *cannot* have them. The only way to falsify this philosophical hypothesis, however, is to produce a predictive theory with universal biological laws. I have proposed such a theory, but it has been presented piecemeal. At the end of this paper, I bring the pieces together into a deductive theory on the evolution of life history traits (e.g. clutch size, mating relationships, sexual size dimorphism).

Key words: induction, deduction, life-history evolution, clutch size, mating relationships, sexual size dimorphism, verification, falsification, laws, *ad hoc* hypotheses.

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I. INTRODUCTION

Many years ago, Plato told a story about a group of men living in a cave. The men were chained in such a way that they could only face the back wall of the cave. Behind the men was a parapet, and behind the parapet was a great fire. Between the parapet and the fire were other men carrying various artificial objects, such as the figures of men and animals carved in wood or stone, which projected above the parapet. What the men in the cave could see were the shadows of the moving objects on the back wall of the cave. This was their reality.

One of the men escaped from his chains and discovered the true causes of the shadows. He found that the shadows on the cave's wall were merely images of the real but unseen objects behind them. He returned to the cave and told of his discoveries. The cave dwellers laughed at him and were determined to resist anyone who came to take them out of the cave.

The message of this story seems to be that the world of appearances – of our perceptions – may be a manifestation of an unseen reality. Einstein &

Infeld (1938: p. 8) expressed the same sentiment when they warned scientists that ‘The discovery and use of scientific reasoning by Galileo ... taught us that intuitive conclusions based on immediate observation are not always to be trusted, for they sometimes lead to the wrong clues’. Galileo invited others to peek through his telescope to see his discoveries for themselves. Some refused; others looked but could see nothing. They were resisting being taken from their cave. Instead of laughing at Galileo, however, they placed him under house arrest for making public his troubling observations.

One of the aims of scientists is to explain what Einstein (1954) called the ‘chaotic diversity of our sense-experience’. There are two broad methods to achieve this goal. The first method was laid out by Francis Bacon. Scientists must first describe nature, the world of appearances, as accurately as possible. In this they are helped by increasingly sophisticated technologies, experimental methods, and statistical analyses. They then discover apparent causal relationships among observables, ‘If A, then B’, such as: ‘If a mammal lives in a cooler climate than another, then it will be bigger’. Investigators seek all

the cases that fall under this rule, and all those that do not, in order to understand better why mammals in cooler climates tend to be larger. The best hypotheses are those in which B always follows A.

Modern physics, however, began with the invention of the deductive method by Galileo and Newton. In thinking about all the facts at hand, a scientist invents a rule by any means whatsoever, often as an inspired guess. Hypotheses of this sort are applied universally and often describe relations among unobservable entities, such as inertia and gravitation. The scientist then deduces the consequences of his rule and determines whether the consequences are verified or refuted by the empirical facts. This is called the deductive-nomological method and is sometimes referred to as the ‘received view’.

The method of biologists today is the inductive method of Bacon instead of the deductive method of Galileo and Newton. Philosophers of science, however, usually equate ‘science’ with physics. Thus, the methods of biologists, which are quite different from those of physicists, with regard to providing explanations for natural phenomena, have been little studied. The purpose of this paper is to draw the attention of biologists to this distinction. The serious question is whether hypotheses concerning unobservables, such as fitness and natural selection, can be considered scientific if investigators cannot deduce empirical facts with them. My contention is that they cannot. In order to explain my reasoning, I draw on the biological, physical, and philosophical literature to show the differences between verification and falsification, induction and deduction, and descriptive and explanatory laws.

Although I am writing about the philosophy of science, I am writing this paper for other biologists from the point of view of a biologist (mainly concerned with ecology and evolution), not from that of a philosopher. My interest has been in finding satisfactory explanations for biological facts rather than in discussing the background philosophical issues. I am interested in discovering laws that allow me to predict what I should see under particular conditions. My first deductive-nomological theories (Murray, 1971, 1979, 1984) were formulated before I had ever heard anything about Karl Popper, other than his insistence that scientific hypotheses should be testable, learned about the deductive-nomological model of Hempel and Oppenheim, and discovered that the search for universal laws in biology was anathema to both biologists and philosophers. As Magee (1997) pointed out, scientists are more

interested in getting on with ‘doing more science’ than worrying about philosophical issues, and, before 1986, in my naïveté, I simply thought I was doing what theoretical scientists were supposed to be doing.

Circumstances forced on me a greater interest in philosophical issues than I might otherwise have had [an editor of my paper (Murray, 1986*b*) suggested that I read Popper]. As a theoretical biologist my particular philosophical interest is in how we scientists should go about evaluating our theories. How do we know that one theory is better than another? I am sure that my colleagues’ interest is the same. Nevertheless, my colleagues and I approach the study of biology in fundamentally different ways, reflecting different philosophies of science, and these may be worth examining.

My biological colleagues seem to be verificationists. They usually propose *ad hoc* hypotheses, which are tested directly by observation or experiment. Sometimes they propose inductive general hypotheses, which more often than not have numerous exceptions. By contrast, with regard to theory structure and evaluation, I am a Popperian in search of universal laws and initial or background conditions from which I can predict or deduce biological facts. I use the deductive-nomological model for structuring syntactic theories. Philosophers seem critical of virtually everything I think and do (as I infer from reading their literature), and they seem equally uncritical of the methods of my colleagues. The question is, whose methods are better at providing satisfactory explanations of biological facts? The answer requires our closely examining the methods used by practising biologists and comparing these with the methods of physicists.

II. A SHORT ARGUMENT

Nobel laureate physicist Richard Feynman has written (Feynman, 1995: p. 2, his italics), ‘The principle of science, the definition, almost, is the following: *The test of all knowledge is experiment.* Experiment is the *sole judge* of scientific “truth”’. Compare this statement with the following statements from the ecological literature:

(1) ‘... as a matter of historical record – it is standard scientific practice to reject ecological data that are in conflict with established theories; ... many contemporary ecological theories are in fact retained – and rightly so – although they are demonstrably wrong; and ... it is by no means obvious

that the proximate goal of theorizing should be to find the truth, hence an important role of mathematics is to provide productive lies' (Fagerström, 1987: p. 258);

(2) '... refutations of [a] theory do not necessarily disprove or invalidate it' (Fahrig, 1988: p. 129);

(3) 'Once the theory has been demonstrated to hold for at least some real ecological systems, it can be considered to be proven' (Fahrig, 1988: p. 131);

(4) 'A scientific discipline like biology ... needs historical explanations which do not systematically follow the methods of investigation of Newtonian physics. Contrary to Murray's [1992*a*] assertions [about Newton's rules of reasoning], his recommendations may serve more to channel, rather than to improve our understanding of the evolution of living things' (Quenette & Gerard, 1993: p. 363);

(5) 'I suggest that the practice of ecology be defined as the interpretation of these patterns and processes by using any approach of human endeavour that generates inspiration among practitioners for further interpretation of pattern and process in nature' (Aarssen, 1997: p. 178);

(6) '... we should stop worrying about whether or not ecology is a purely empirical science and just accept that, in practice, it is not' (Aarssen, 1999: p. 375); and

(7) 'Like many other authors ... , I find the narrow emphasis on hypothesis testing counter-productive' (Turchin, 1999: p. 155).

These statements hardly reflect the same respect for data that was expressed by Feynman. Apparently, these ecologists believe that whatever an ecologist is allowed to think can be independent of the available data. They seem to provide support for Feyerabend's (1975) principle that 'anything goes' in science. Can we say that such an attitude is scientific? I think that we cannot.

We have no reason to believe that these views are representative of the thinking of most biologists, but we have no reason to believe otherwise. Few have explicitly expressed a philosophy like that of Feynman, although a few have commented on the inadequacy of ecological and evolutionary theory (Murray, 1975, 1986*a, b*, 1992*a*; Dayton, 1979; Pielou, 1981; Simberloff, 1983; Stenseth, 1983; Loehle, 1987; Peters, 1991; Weiner, 1995; O'Connor, 2000). Thus, if we accept Feynman's description of what a science is, then, judging from these quotations, we should have doubts about whether theoretical biology is a science. Our evaluation of theoretical biology, however, should not rest on these few expressed statements and the fact that

most scientists do not explicitly discuss their philosophy. Their philosophy shows in the way they do science.

III. WHAT IS THE SCIENTIFIC METHOD OF BIOLOGISTS?

If we regard the few quotations in the previous section as unrepresentative, we may ask, what, then, is the scientific method of biologists? The description of the scientific method in virtually every introductory biology textbook gives the impression, without using the terms, that biologists are logical positivists and test their hypotheses according to the verification principle. According to the textbooks, scientists first make observations and collect data about the world around them. They then propose a hypothesis. More facts are gathered to test the hypothesis. As facts accumulate confirming (i.e. verifying) it, scientists eventually call the hypothesis a theory. With further tests scientists may elevate the hypothesis/theory to the status of law. This method is induction.

Of the textbooks I have at hand, one example of the scientific method describes biologists hypothesizing that the nucleus was essential for the well being of a cell (Solomon *et al.*, 1993). Biologists tested this hypothesis by removing the nuclei from amoebae in a controlled experiment. Sure enough, the amoebae without nuclei died and those with nuclei survived, 'confirming' the hypothesis. Another example was Charles and Francis Darwin's hypothesis that the tip of a stem of a plant detected the direction of light, towards which the plant then grew (Campbell, 1987). The Darwins removed the tips of some plants, covered others with tinfoil, and showed that only the intact plants grew toward the light.

A nearly universal textbook example of the scientific method is Pasteur's experimental demonstration that life did not generate spontaneously, giving some credence to one tenet of the so-called cell theory – 'all cells arise from preexisting cells' (Keeton, Gould & Gould, 1993; Solomon *et al.*, 1993; Brum, McKane & Karp, 1994). The other tenets are 'all organisms are composed of one or more cells' and 'the cell is the basic organizational unit of life'. A moment's reflection reveals that each of these is an inductive generalization, confirmed by repeated observations.

Keeton *et al.* (1993: p. 3) describe the biologists' inductive scientific method, 'The step from isolated bits of data to generalization can be taken with confidence only if enough observations have been

made to give a firm basis for the generalization, and then only if the individual observations have been reliably made'.

Only one textbook mentions deduction (Solomon *et al.*, 1993). The authors, who refer specifically to the syllogism, state that deductive reasoning proceeds from general principles to specific conclusions and, therefore, results in a decrease in information content. Such a view also appears in an introductory philosophy text (Salmon, 1989). These authors do not discuss the deductive method of Popper, much less that of Newton, Einstein, Bohr, Feynman, and many other physicists, whose general laws, when applied under a variety of initial conditions, produce a deductive theory with an enormous information content.

Inasmuch as biologists are not introduced to the scientific method of Newton, Einstein, Bohr, Feynman, and Popper, it is no wonder that they follow the inductive method of Bacon, taught in virtually every textbook and practiced by virtually every biologist. The evidence indicates that biological explanation relies on *ad hoc* hypotheses and induction. Rensch (1971: p. 131, his italics) noted that 'there are exceptions to almost every established biological law. Such laws are therefore generally described only as *rules*'. Rensch (1971) identified 100 biological rules, which vary from the general (p. 133), 'All organisms produce a superabundance of progeny, of which the majority (often over 99 percent) die before reaching sexual maturity. This overproduction causes selection to become especially intensive', to the quite specific (p. 137), 'Large beetles show more marked morphological sexual differentiation than related smaller species'. Most of these 100 rules are generalizations inferred from observations by induction. Nevertheless, from these rules, biologists are able sometimes to make good 'predictions' (Rensch, 1960: p. 110, his italics):

We may best elucidate the effect of these rules by estimating how far we may *predict* the structure and functions of a warm-blooded new species, which will be discovered in the future.

A. EXAMPLE: If a songbird is discovered in tropical Brazil which is closely related to a species of the same genus in North America, we may predict with about 70–100 per cent probability that this tropical species will show the following characters: (1) smaller size, (2) relatively longer bill, (3) relatively longer feet, (4) relatively longer tail, (5) more roundish shape of the wings, especially the first and third to fifth primaries relatively shorter, (6) less dense feathers or less duneparts [*sic*], (7) feathers with more melanin, (8) less eggs per

clutch, (9) without inherited migratory instinct, (10) differences in relative size of interior organs (depending also on body size), (11) differences in metabolism (also depending on special body size), (12) shorter life-span.

No doubt, good naturalists can make such 'predictions' (actually 'expectations') based on their knowledge of *ad hoc* correlations between features of animals and features of the environments, such as Bergmann's rule, Allen's rule, and many other rules recounted by Rensch, but these rules are *ad hoc* hypotheses generalized by induction. The problem with these 'predictions' is that their refutation does not change the acceptability of the rules from which they were 'deduced'. (To be explicitly clear, biologists do not usually use the word prediction to mean a forecast of some future event because we are quite certain that the future cannot be predicted. Nevertheless, biologists often write, 'Natural selection predicts ...', 'Life-history theory predicts ...', or the all-purpose 'Theory predicts ...'. As already indicated, a prediction for biologists is usually an expectation based on empirical correlations.)

A more sophisticated form of induction has been described explicitly as the deductive scientific method. Taylor & Williams (1984: p. 2264), for example, suggested that 'The power-function dependence of biological rates has been recognized as "... one of the few manifestations of a universal law in biology"' (Platt and Silvert, 1981)'. Peters (1983, 1991) provided many examples of the power-function relations of rates from the fields of ecology and physiology. Although nominally a strong supporter of using Popper's philosophy in ecology, Peters (1983, 1986, 1991) got Popper's method wrong. Peters (1983: p. 2, his italics) stated,

Scientific theories predict by suggesting the probable nature of one thing, called the *dependent variable*, on the basis of some other thing, called the *independent variable*. ... To achieve prediction, a theory must describe or imply how to ascertain the value of the independent variable. The body of the theory then tells us how to use this value to arrive at a probable value or range of values for the dependent variable. When this is done, a prediction has been made.

We can understand Peters's notion of theory better than that of many authors because he provides explicit examples of his 'deductive' method (Peters, 1983, 1991). For example (Peters, 1983), after physiologists measured the time spent sleeping each day by various species of herbivorous mammals, they plotted the time spent sleeping against body mass. With the fitted regression equation describing the relationship, physiologists could predict the time

Table 1. Ad hoc hypotheses explaining clutch-size variations in birds

Hypothesis	Authority
Food limitation	Lack (1947, 1948a, 1954, 1968)
Resource allocation	Cody (1966)
Protein limitation	Drobney & Fredrickson (1985)
Lipid limitation	Ankney <i>et al.</i> (1991)
Nest predation	Skutch (1949); Slagsvold (1982); Martin (1992)
Cost of reproduction	Williams (1966); Charnov & Krebs (1974)
Protection of young	Safriel (1975)
Nest size	Snow (1978); Slagsvold (1982)
Individual optimization	Högstedt (1980); Pettifor <i>et al.</i> (1988)
Egg viability	Arnold <i>et al.</i> (1987)
Bet-hedging	Kozlowski & Stearns (1989)
Progeny choice	Kozlowski & Stearns (1989)
Renesting	Milonoff (1989, 1991)
Exertion	Milonoff (1991)
Insurance	Forbes (1990)

Table 2. Hypotheses regarding the hatching patterns of birds' eggs in nests (Stoleson & Beissinger, 1995; Slagsvold *et al.*, 1995)

Hypothesis	Prominent authority
Energy constraints	Greig-Smith (1985); Slagsvold (1986)
Hormone	Mead & Morton (1985)
Egg viability	Arnold <i>et al.</i> (1987)
Egg protection	Oring (1982)
Limited breeding opportunities	Beissinger & Waltman (1991)
Brood parasitism	Kendra <i>et al.</i> (1988); Lombardo <i>et al.</i> (1989)
Brood reduction (a.k.a. resource tracking)	Lack (1947, 1954)
Insurance egg	Stinson (1979); Cash & Evans (1986)
Sex ratio manipulation	Slagsvold <i>et al.</i> (1986)
Peak load reduction	Hussell (1972)
Dietary diversity	Magrath (1990)
Hurry-up	Hussell (1972); Slagsvold (1986)
Sibling rivalry	Hahn (1981)
Larder (a.k.a. ice box)	Alexander (1974)
Sexual conflict	Slagsvold & Lifjeld (1989)
Nest failure	Hussell (1972)
Adult predation	Magrath (1988)

spent sleeping of other species of herbivorous mammals. 'Such [future collections of] data, once collected, can be used to test the theory by comparing the new data with the quantitative description. If the two are not statistically different, the theory is confirmed or corroborated. If they are different, the theory has been disconfirmed or falsified. ... Should the theory be falsified, one has a number of options. The simplest is to build a new statistical description based on all observations (old and new) and to begin the process again' (Peters,

1983: p. 5). Alternatively, one can either search for the causes of the discrepancies or give up on generality. 'In the latter case, one has not abandoned theory but has replaced a general, but inaccurate, theory with a host of more specific theories that one hopes can predict better' (Peters, 1983: p. 5).

What Peters describes is the inductive method, no different from that used in determining whether 'all swans are white'. He has collected some instances, generalized them by induction into a 'theory', and tested the theory by searching for additional

Table 3. A classification of mating systems (Wittenberger, 1979)

General classification	Spatial classification	Temporal classification
1. Monogamy	A. Territorial monogamy B. Female-defence monogamy C. Dominance-based monogamy	A. Serial monogamy B. Permanent monogamy
2. Polygyny	A. Territorial polygyny B. Harem polygyny	A. Successive polygyny B. Simultaneous polygyny
3. Polyandry	A. Territorial polyandry B. Nonterritorial polyandry	A. Successive polyandry B. Simultaneous polyandry
4. Promiscuity	A. Broadcast promiscuity B. Overlap promiscuity C. Arena promiscuity D. Hierarchical promiscuity	

instances that verify it. This is no different from searching the world for additional swans. The greater sophistication of a regression line bordered by statistical confidence limits seduces biologists into thinking that they are doing more – that they are engaged in deductive science.

So, biology lacks laws like those of physics, laws that are not only universal but also predictive and explanatory. Inductive generalizations, even if very good at predicting, are descriptive, not explanatory. ‘All swans are white’ does not tell us why swans are white. An equation that tells us that small mammals spend more time sleeping than big mammals does not tell us why. Deductive theories, in contrast, such as Newton’s Laws of Motion, the Theory of General Relativity, and the Theory of Quantum Electrodynamics, tend to encompass a wide range of seemingly disparate phenomena, and they seemingly provide explanations for why the physical world is the way it is.

The nature of biological hypotheses becomes apparent when we realize that refutations do not lead to their death. Evolutionary biologists, in particular, accumulate long lists of *ad hoc* hypotheses, each one applicable to one or a few species or situations (see Tables 1–3). Sometimes this is explicit. For example, Ankney, Afton & Alisauskas (1991: p. 1031) stated, ‘We are unaware of data from waterfowl that are inconsistent with the “Egg Production Hypothesis.” Thus, we urge critics of the EPH to attempt to refute it in the “old fashioned way.” That is, obtain data from waterfowl; according to the AOU checklist, coots do not qualify!’. Of course, not all species of waterfowl (ducks, geese, and swans) have been tested. If an investigator obtained data from a waterfowl species that was

inconsistent with the EPH, I have no doubt that the EPH would not be rejected (after all, it may be true for the species so far examined). As Peters (1983) pointed out, we have a number of options, none of which suggested that the theory be considered refuted (see above). This attitude may be justified inasmuch as the EPH is a descriptive hypothesis about a proximate factor limiting the number of eggs laid by a female at any time. It could be true for some species, but not for others. *Ad hoc* hypotheses that identify the proximate (environmental) factor(s) determining a particular clutch’s size, however, should not be confused with hypotheses that identify the ultimate (evolutionary) factor(s) affecting the mean clutch size of a population.

I am not arguing that the biologists’ inductive generalizations are not science. Every science must start this way, describing and organizing the apparent facts into patterns. Furthermore, most scientists are engaged in what Kuhn (1962) characterizes as normal science. They are solving puzzles that bring experience into line with prevailing theory. Few physicists in the eighteenth and nineteenth centuries were expecting to bring down Newton’s theory with their experiments. Revolutions occur only infrequently in science, and few scientists have the opportunity to conduct the crucial experiment or make the crucial observation that swings scientific opinion in favour of a new theory. An individual investigator’s failure to solve a particular problem is often taken as his or her personal failure in designing and carrying out the experiment, rather than a failure of the theory (Kuhn, 1970). Nevertheless, each puzzle solved lends further support for a theory.

Biologists, by contrast, are not testing the hy-

pothetical consequences that have been logically deduced from the laws of some theory, if only because they recognize no Newtonian-like biological laws. As a result, they simply ‘test’ *ad hoc* hypotheses, which develop out of their experience and which are within the acceptable range of answers to puzzles within the metaphysical research program called natural selection. They are often answering the question, ‘How do I explain my data in terms of the theory of natural selection?’ (Murray, 1986*b*, 1991*b*).

This state of affairs in biology, the Baconian exploration of nature, is perfectly justifiable as long as the investigators understand that they are not doing deductive science. What I am arguing is that biologists and philosophers of biology eschew a research method that has been so successful in physics – the deductive method so articulately described by Popper (1968, 1979, 1989). Some biologists excuse their failure to develop such laws and theory by claiming that biological systems are far more complex than physical systems (Stebbins, 1977; Quinn & Dunham, 1983; Bartholomew, 1986; Slobodkin, 1988; Mayr, 1996; Begon, 1998; Lawton, 1999). Some biologists claim that the deductive method of the physicists is inappropriate for evolutionary theory, which is essentially a historical science (Mayr, 1982, 1991, 1996). Furthermore, biologists presume that the deductive method implies determinism, a philosophy they reject (Mayr, 1982, 1988, 1991; Rose, Kamin & Lewontin, 1984). Thus, for them, deduction is inappropriate in biology because the future cannot be predicted.

The issue would seem to be whether biologists should be able to develop a predictive theory with universal laws. To hypothesize that they cannot because they have not (or for any other reason) is an inductive inference in itself. I happen to think that this hypothesis is wrong.

I contend that biologists and philosophers of biology are wrong when they say that Newtonian-like universal laws and predictive theory are inappropriate in biology. Before presenting a predictive biological theory with universal laws, I am going to argue that Newton’s Theory of Motion is a model explanatory scientific theory, that the deductive-nomological model of Hempel & Oppenheim (1948) is useful for constructing predictive theory, and that the falsificationist principle of Popper (1968, 1979, 1989) is necessary for evaluating theory. I accept the views of Newton, Einstein, Feynman, and Popper as the way of doing science, not because I suffer from ‘physics envy’

(Cohen, 1971; Egler, 1986; Begon, 1998), but because I think that logic transcends subject matter. Physics simply provides excellent illustrative examples of the method. I use these methods because, as a theoretical biologist, I see no other way of proposing and testing predictive, explanatory theories.

Progress in science occurs in three stages: discovery, justification, and acceptance. There are no rules or methods that guarantee discovery. Through hard work and luck a scientist may discover a new species, structure, relationship, behavior, law, or whatever in nature. The scientist must then justify his or her discovery. This may be rather straightforward in the case of a new species or structure. Justifying new explanations (such as inertia or natural selection, which cannot be seen) is more difficult and involves the rules of logic. Why one scientist accepts a new theory when another does not is not easy to explain, being a psychological phenomenon. Each thinks the other is doing bad science, even when both are exposed to the same observations and arguments. Again, there are no rules.

In this paper, we are concerned only with the justification of theory, that is, with the logical arguments by which we justify why we think what we think.

IV. THE PROBLEM THAT BIOLOGY POSES FOR PHILOSOPHY

The fact that biology lacks the kind of universal laws and predictive theory that characterizes physics poses a serious problem for both biologists and philosophers. Biology is certainly a successful science. Biological theories are certainly explanatory to the satisfaction of many of its practitioners, even if they are not predictive. According to what has become called the ‘received view’, the method of theoretical physicists, we should expect a causal explanation to include at least one universal law. How then do we justify biological explanations, which do not include laws, much less predictions deduced from laws? Biologists, of course, pay little attention to the problem. They just get on with doing more science because this is what they do. Philosophers, however, spend more than a little time discussing the problem because this is what they do.

One reason for the diversity of views among biologists and philosophers is that there seems to be no alternative to the unpredictable but very explanatory neo-Darwinian formulation of evolution-

ary theory. Biology has no deductive-nomological model of evolutionary theory. Lewontin (1972: p. 181), for example, declared, ‘The trouble ... is that even though natural selection might not be an epistemologically satisfactory hypothesis, it might nevertheless be true. Very inconvenient, but there you are’. With unusual candor, however, Lawton (1999) proposed a novel possibility for the lack of predictive laws in ecology – a lack of imagination and courage among its practitioners. I think this is the correct explanation (Murray, 2000*c*). As I have stated before (Murray, 1975; Jehl and Murray, 1986), once a person is convinced that universal laws are impossible in biology, he is unlikely to look for, much less discover, one. The literature read by young biologists is incessantly pessimistic about their ever discovering a deductive-nomological theory of natural selection, or anything else. Why should anyone devote his or her energy and career to what everyone agrees is a fruitless task?

Nevertheless, much of what biologists do is good science. What I am arguing is that biologists, who are ignoring if not deprecating the deductive method, may be missing insights into biological phenomena that could be provided by universal laws and predictive theory. At the very least, a theory of evolution, complete with laws, initial conditions, and predictions could reduce the criticisms leveled at biology and, especially, the scientific status of its central unifying principle, natural selection.

What is required to settle these arguments, of course, is an example of a biological theory in syntactic form with laws, initial conditions, predictions deduced from the laws and initial conditions, and empirical facts that verify the predictions. I provide such a theory in Section IX. One essential feature of the deductive-nomological method is that a theory should be evaluated by comparing its predictions with empirical facts rather than dismissed because conventional wisdom considers such theories to be impossible or inappropriate for biology. Before considering the life-history theory, let me specify exactly what I mean by a satisfactory scientific theory (a syntactic, deductive-nomological, Popperian theory) by reviewing a successful, if not absolutely correct, physical theory.

V. A MODEL THEORY IN THE RECEIVED VIEW

The aim of science, according to Popper (1979: p. 191, his italics), is ‘to find *satisfactory explanations*, of whatever strikes us as being in need of explanation’.

He (Popper 1979: p. 191, his italics) suggested that a satisfactory causal explanation includes ‘a set of statements by which one describes the state of affairs to be explained (the *explicandum*) while the others, the explanatory statements, form the “explanation” in the narrower sense of the word (the *explicans* of the *explicandum*)’.

A satisfactory *explicans* must include at least one universal statement and ‘have a variety of testable consequences which are different from the *explicandum*’. We justify the laws leading to *explicandum* A (which followed from the laws and initial conditions A) by showing that deduced *explicandum* B (following from the laws and initial conditions B) is empirically true. Furthermore, the *explicans* of the *explicandum* can be tested only ‘if we confine ourselves to universal laws which are ... falsifiable’ (Popper, 1979: p. 193).

Popper’s philosophical description of how physicists approach their understanding of nature is exactly how theoretical physicists go about their work, as described, for example, by Feynman (1965: p. 156),

In general we look for a new law by the following process. First we guess it. Then we compute the consequences of the guess to see what would be implied if this law that we guessed is right. Then we compare the result of the computation to nature, with experiment or experience, compare it directly with observation, to see if it works. If it disagrees with experiment it is wrong. In that simple statement is the key to science. It does not make any difference how beautiful your guess is. It does not make any difference how smart you are, who made the guess, or what his name is – if it disagrees with experiment it is wrong. That is all there is to it.

Perhaps Popper’s most important contribution to the philosophy of science was his recognition that certain scientific statements could not be verified, in contrast to the logical positivists, who required that scientific statements be verified by empirical evidence. For example, the statement, ‘all swans are white’ can be tested by direct observation. It is verified and gains credibility every time we see another white swan, until it is shown to be false when we finally see a black swan in Australia. Other statements, which scientists have no doubt are unquestionably scientific, such as Newton’s First Law of Motion, could not conceivably be verified. As Einstein & Infeld (1938: p. 8) pointed out,

[Galileo’s] law of inertia cannot be derived directly from experiment, but only by speculative thinking consistent with observation. The idealized experiment can never be actually performed, although it leads to a profound understanding of real experiments.

Such unverifiable statements, however, are capable of being falsified. They could be shown to be false by logically deducing their consequences, and comparing the latter with empirical facts. Verifying the consequences does not verify the assumptions, whereas showing that the consequences are untrue falsifies the assumptions. Verifying the consequences only allows us to state that the assumptions – the laws – of the theory have not yet been falsified.

Now, let us assume that Newton’s Theory of Motion exemplifies what Popper means by a ‘satisfactory explanation’ in science. If so, we should discuss Newton’s theory to see how it meets Popper’s and Feynman’s criteria of a satisfactory scientific theory before evaluating biological theories by these criteria (ignoring, for the moment, that Newton’s theory has been falsified by the motions of Mercury and superseded by Einstein’s General Theory of Relativity). In order to illustrate the deductive-nomological method, let us imagine how Newton may have gone about formulating his great theory [the story is told in greater detail and more accurately by Cohen (1980)].

Suppose that Newton wanted to explain why the planets moved around the sun. Newton already knew *how* they moved from Kepler’s laws of planetary motion, but Kepler’s laws did not explain *why*. Newton put his argument in what we now may identify as the deductive-nomological model of Hempel & Oppenheim (1948) – whom I will henceforth follow by substituting *explanans* for *explicans* and *explanandum* for *explicandum*,

$$\left. \begin{array}{l} L_1, L_2, \dots, L_k \text{ hypotheses} \\ C_1, C_2, \dots, C_r \text{ initial conditions} \\ \hline E \end{array} \right\} \begin{array}{l} \textit{explanans} \\ \textit{explanandum} \end{array}$$

In this model, we may denote Newton’s first law of motion as L_1 , second law of motion as L_2 , third law of motion as L_3 , and law of gravitation as L_G . The initial conditions, often information that is already known, such as the radius and period of the moon’s orbit, we denote as C_1, C_2, \dots, C_r . From these laws and a particular set of initial conditions, Newton was able to deduce the motions of the planets. He showed, however, that Kepler’s Laws were true only as approximations, and, therefore, were ‘strictly invalid’ (Popper, 1979; Cohen, 1980). Not only did Newton’s analysis give us a quantitatively better understanding of the planetary motions, but with Newton’s theory we could now say that the planets move as they do because of the interaction of inertial

motion and gravitation, because the forces acting on a moving body are equal to the product of the mass and acceleration of that body, that the centrifugal force pulling the planets away from the sun was, in each case, equal to the gravitational force attracting the planets toward the sun, and that, in each case, the gravitational force was directly proportional to the product of the masses of the sun and planet and indirectly proportional to the square of the planet’s orbit’s radius. [We might also want to know why two massive bodies attract one another as they do. On this Newton refused to guess (‘Hypotheses non fingo’), simply because he had no evidence to support whatever guess he might have. Universal laws do not predict or explain everything that we might like to know.]

So, Newton has constructed a theory that explains the motions of planets. He has done what he set out to do – to provide what is for him a satisfactory explanation for planetary motion. Nevertheless, the evidence in support of the *explanans* is the *explanandum*, which is a circular argument because the evidence for the explanation is the facts that Newton set out to explain. This is not enough. At this point, the explanation is *ad hoc*. It explains what it set out to explain. To avoid being *ad hoc*, Newton must deduce from his universal statements (i.e. his laws) a variety of singular statements that are other than that or those contained in the original *explanandum*. From the laws, Newton must deduce consequences different from what he wanted to explain in the first place.

Newton did this by predicting the consequences of additional sets of initial conditions. The initial conditions refer to something that he already knew – say the radius and the period of the moon’s orbit around the earth. With his laws and these initial conditions, Newton solved the ‘moon problem’ (Rogers, 1960; Cohen, 1980). He deduced that a body near the earth’s surface should fall approximately 16.1 feet (he was more precise and used an old linear measure, Paris feet) in the first second of free-fall. This deduction is verifiable. All he needed to do was to get a long ladder and to time the fall of an apple from 16.1 feet. He did, and the apple fell close enough to 16.1 feet in the first second of free-fall *not to falsify* his theory. [In the *Principia*, Newton (1729) tested the prediction with data on the swing of a pendulum.] It should be clearly understood that *verifying* the prediction deduced from the *explanans* does not verify Newton’s laws. According to Popper, all we can say is that Newton’s Laws have not yet been falsified. With additional initial conditions, Newton’s theory predicted the shape of the earth

(i.e. flattened at its poles), the daily cycle of two high and two low tides, the precession of the equinoxes, the orbits of comets, and much more.

Subsequently, in 1758, using Newton's laws, Halley predicted the appearance of a comet, later to bear his name, and, in 1846 Adams and Le Verrier independently predicted the position of an unknown planet, now known as Neptune. Each of these predictions was verified to be true. Thus, we can say that we have verified the predictions – we have shown them to be true – but, again, verifying the predictions does not verify the laws. All we can say about the laws is that they have not yet been falsified, that is we have not yet deduced a prediction that has been shown to be false.

Newton's theory was eventually falsified by the observation of Mercury's precessing orbit. We now accept Einstein's General Theory of Relativity as a better explanation of the physical facts than Newton's because it not only accounts for Mercury's orbit but for many other physical facts (Will, 1986).

In practice, predictions often are of the initial conditions (Putnam, 1991). Suppose that Newton already knew (which seems plausible) that an apple near the earth's surface fell 16.1 feet in the first second of free-fall. He could have asked himself, 'What initial conditions could I find that, in combination with the laws, will allow me to deduce the apple's behaviour?' His imagination led him to consider the period and radius of the moon's orbit. Scientists are often confronted with explaining already known facts with an already proposed theory. They essentially predict the initial conditions, and then perform the experiment to show that the application of the laws under the specified initial conditions does result in the observation that needed explaining. The deductive-nomological model is a description of the structure of a logical theoretical argument, not a prescription of the sequence of thought a scientist must follow in developing a scientific explanation.

Experimental physicists, however, delight in making new observations that current theory has not predicted (Lederman & Teresi, 1993). This sends theoreticians scurrying back to their drawing boards. Either they discover overlooked initial conditions or overlooked consequences that account for the new observation. If they cannot do this, they create a new theory – but not necessarily immediately. Theory construction is a creative process. Scientists do not immediately reject a theory, which otherwise successfully explains a wide range of observations, because of one or two anomalies. They keep a flawed

but otherwise useful theory until a better alternative is proposed. Currently, the general theory of relativity is looking pretty good (Will, 1986). Scientists are also aware that this theory will one day be superseded (Einstein himself tried to find a better, more inclusive theory), but that is not sufficient reason to reject it.

Before leaving our discussion of Newton, we should mention the role of imagination in science. What can be the empirical facts that led Galileo to the idea of inertial motion and Newton to the First Law of Motion? Why should anyone believe that inertial motion should be in a straight line at a constant speed? Inertial motion was a bold guess. Galileo, though, not only guessed that inertial motion was in a straight line but that the straight line was always tangential to a circle whose center was the earth's center (Santillana, 1955; Cohen, 1985). Thus, for Galileo the moon's motion was caused solely by inertial motion.

Inertial motion, by whomever's conception, is necessarily abstract. What does observation tell us about inertia? Nothing. Einstein & Infeld (1938) give us an idea of what Galileo may have been thinking. Suppose we take a cart and give it a push. It will move some distance, slow down, and come to a stop. Suppose that we smooth the road, streamline the cart, and then give the cart a push. It will move further, but it will nevertheless come to a stop. No matter how often we do the experiment, we get the same result. One could justifiably conclude that 'a moving body comes to a standstill when the force which pushes it along can no longer so act as to push it'. Now, this is Aristotle's hypothesis (Einstein & Infeld, 1938), which has been repeatedly verified. Aristotle, however, was wrong. How did Galileo come to a different conception? Einstein & Infeld (1938) suggested that Galileo asked, how is it possible to increase the distance that the cart goes before stopping? He noticed that after he streamlined the cart and smoothed the road, the cart moved further. Suppose, Galileo thought, there were no impeding forces. He guessed that the cart would move in a straight line at a constant speed forever, an idea that was completely contrary to experience. Aristotle's conclusion regarding the nature of motion was consistent with appearances, but the appearances gave him 'false clues'.

Curiously, some biologists think that the Popperian method constrains imagination, 'There is no prescription for progress in limnology or ecology, although progress can be stifled by restricting the limits of creative thought. Those who embrace

constraints crafted by others in the form of Popperian or hypothetico-deductive straightjackets may have divined a means to restrict the imagination, but there is no evidence in my view that those constraints encourage breakthroughs in biological sciences' (Lehman, 1986: p. 1161), a view seconded by Roughgarden, May & Levin (1989). Feynman (quoted in Gleick, 1993: p. 324, original italics), however, pointed out that 'The whole question of imagination in science is often misunderstood by people in other disciplines. They overlook the fact that whatever we are *allowed* to imagine in science must be *consistent with everything else we know ...*'. There are, then, no constraints on imagination when a scientist invents an explanatory theory. The constraint is on the testing of these inventions as scientific explanations.

Finally, biologists tend to believe that physics is simpler than biology (e.g. Stebbins, 1977; Quinn & Dunham, 1983; Bartholomew, 1982, 1986; Slobodkin, 1988; Begon, 1998), allowing them to believe that universal laws and deductive theory are inappropriate in biology. But this is a misunderstanding. In fact, the physical world is extraordinarily complex. What physicists do for the physical world, which biologists do not do for theirs, is to simplify it in order to study it.

For example, as Newton (quoted in Cohen, 1980: p. 265) pointed out,

... the orbit of any one planet depends on the combined motion of all the planets, not to mention the action of all these on each other. But to consider simultaneously all these causes of motion and to define these motions by exact laws allowing of convenient calculation exceeds, unless I am mistaken, the force of the entire human intellect.

Thus, Newton's mathematical model has only one planet orbiting a point in space; his physical model has only one planet revolving around one star. And Newton was correct; the three-body problem has not yet been solved. A more recent physicist, Richard Feynman (1995: p. 23), told us

The things with which we concern ourselves in science appear in myriad forms, and with a multitude of attributes. For example, if we stand on the shore and look at the sea, we see the water, the waves breaking, the foam, the sloshing motion of the water, the sound, the air, the winds and the clouds, the sun and the blue sky, and light; there is sand and there are rocks of various hardness and permanence, color and texture. There are animals and seaweed, hunger and disease, and the observer on the beach; there may be even happiness and thought. Any other spot in nature has a similar variety of things and

influences. It is always as complicated as that, no matter where it is.

How could anyone guess that these appearances were all manifestations of various combinations of a few elementary particles? More specifically, with regard to the theory of quantum electrodynamics, to which he contributed and for which he shared the Nobel Prize, Feynman (1985: p. 8, his italics) wrote, I must clarify something: When I say that all the phenomena of the physical world can be explained by this [QED] theory, we don't really know that. Most phenomena we are familiar with involve such *tremendous* numbers of electrons that it's hard for our poor minds to follow that complexity. In such situations, we can use the theory to figure roughly what ought to happen and this *is* what happens, roughly, in those circumstances. But if we arrange in the laboratory an experiment involving just a few electrons in simple circumstances, then we can measure it very accurately, too. Whenever we do such experiments, the theory of quantum electrodynamics works very well.

The physical world is not simple. Physicists simplify the physical world in order to study it. Biologists do not simplify the biological world. As Dyson (1988: pp. 45–46) put the difference, 'Unifiers are people whose driving passion is to find general principles which will explain everything. They are happy if they can leave the universe looking a little simpler than they found it. Diversifiers are people whose passion is to explore details. ... They are happy if they leave the universe a little more complicated than they found it. ... Biology is the natural domain of diversifiers as physics is the domain of unifiers'.

VI. RESPONSE TO CRITICISMS OF DEDUCTIVE THEORY: A SCIENTIST'S VIEW OF PHILOSOPHY

As I indicated above, I am a Popperian (concerning the evaluation of universal explanatory laws). Philosophers of biology (Ruse, 1973, 1977, 1981; Hull, 1974; Sober, 1984, 1993; Kitcher, 1985; Lloyd, 1988; Thompson, 1989) and philosophizing biologists (Rensch, 1971; Caplan, 1981; Bartholomew, 1982, 1986; Quinn & Dunham, 1983; Roughgarden, 1983; Diamond, 1986; Lehman, 1986; Slobodkin, 1986; Mayr, 1988, 1996; Mentis, 1988; Roughgarden *et al.*, 1989; Pickett, Kolasa & Jones, 1994), however, either ignore or reject Popper's philosophy. The received view, however, with its universal laws, initial conditions, and the predictions deduced from them, as exemplified by Newtonian

theory and as described by Popper, Einstein, Feynman, and many others, has been a successful way to conduct scientific research. Even if there are other ways to investigate nature (and I believe that there are), their existence does not seem sufficient reason for biologists to *reject* a method of study so successfully used by physicists. I am at a loss to understand why the logic of Popper, the deductive-nomological structure of theory, and the received view have generated so much criticism.

(1) Popper and logical positivism

A commonly held notion among biologists and philosophers of biology is that Karl Popper was a logical positivist or logical empiricist, terms that are not distinguished by Passmore (1967) or Friedman (1998), or in Audi (1995) and Honderich (1995). He was not. This misunderstanding may have been caused by the manner in which his ideas were first published (in a mainly positivistic series edited by logical positivists), which, according to Popper (1976: p. 87), ‘had some curious consequences. One was that until its English publication in 1959 ... philosophers in England and America ... seem to have taken me for a logical positivist – or at best for a dissenting logical positivist who replaced verifiability by falsifiability. Even some logical positivists themselves ... preferred to see in me an ally rather than a critic’. Jarvie (1998) pointed out that ‘Popper’s attacks on central logical positivist contentions contributed to the demise of that movement’. The point could have not been put more strongly than by Magee (1973: p. 49), who knew Popper well (Magee, 1997), ‘Popper was never a positivist of any kind; quite the reverse, he was the decisive anti-positivist, the man who put forward from the beginning the arguments that led (after an excessively long time) to logical positivism’s dissolution’.

The belief that Popper was at one time a logical positivist or logical empiricist, however, persists to the present day. For example, Boyd (1991) suggests that Popper’s falsificationism was ‘a variation on the empiricist solution to the demarcation problem’, and Friedman (1998) contends, without explanation, that Popper was, ‘at least for a time, closely associated with logical positivism’. Popper (1976), however, insisted that ‘I was always an adherent of *realism*’ (p. 20, his italics), and ‘It was mainly in discussions with [Gompertz] that I began to stress my realism, my conviction that there is a real world, and that the problem of knowledge is the

problem of how to discover this world. I became convinced that, if we want to argue about it, we cannot start from our sense experiences ... without falling into the traps of psychologism, idealism, positivism, phenomenalism, even solipsism – all views which I refused to take seriously’ (pp. 75–76).

O’Hear (1989), following Hacking (1983), summarized ‘six key ideas characteristically associated with a positivistic approach to natural science’. These included hostility to causes, a ‘thoroughgoing’ hostility to unobservable or theoretical entities, and an opposition to metaphysics. Logical positivists held ‘that a rigorous description of all nature can be pieced together, like a gigantic tinker-toy, out of small units of fact, each of which can be separately verified to be so’ (Bronowski, 1965: p. 35), and logical empiricism ‘[insisted] that all significant statements must have experiential import, that the latter consists in suitable data of direct observation, and that sentences which are entirely incapable of any test must be ruled out as meaningless “pseudo-hypotheses”’ (Hempel, 1965: p. 125). [See also Passmore (1967), Fotion (1995), Fumerton (1995), and Magee (1997) for characterizations of logical positivism.] According to Magee (1997: p. 46), the publication of Popper’s *Logik der Forschung* ‘spelled total shipwreck for logical positivism’. And Popper (1976) himself claimed to have been responsible for ‘killing’ it. Popper did not transform it. He killed it.

(2) Hempel and logical positivism

Carl Hempel has been described as ‘One of the leaders of the logical empiricist movement’ (Ruse, 1995). Although Hempel was a student member of the Vienna Circle (Hempel, 1993), which spawned logical positivism, his later writings (Hempel, 1965, 1966) give the impression that he challenged some important positivist concepts. For example, he makes a strong case for the reality of theoretical entities (Hempel, 1966: pp. 77–82). Furthermore, the deductive-nomological model itself, incorporating laws referring to unobservables and theoretical entities and providing indirect tests of statements, cannot easily be construed to be part of the logical positivist philosophy. Hempel seems to have changed his mind regarding several of the logical positivists’ central principles.

(3) Logical positivism still lives

Despite some philosophers’ pronouncements to the contrary, logical positivism and logical empiricism

seem to be alive and well, as indicated above, in the verificationist philosophy of biologists. Peters (1976: p. 1) is rather explicit: 'My criteria for the acceptance of a scientific theory are derived from the logical positivists', even though he is a proponent of deductive and falsificationist methods (Peters, 1983, 1991), as he mistakenly understood them (see discussion above). Also logical positivism or logical empiricism is still featured in the discussions of philosophers of biology (Ruse, 1973; Hull, 1974; Wilson, 1985; Lloyd, 1988; Thompson, 1989). For example, Thompson (1989: p. 23) claims that the received view 'has its roots in logical positivism', Lloyd (1988: p. 16) refers to 'the received (logical positivist) view', and, most explicitly, Hull (1974: pp. 2–3) states, 'central to the logical empiricists' conception of science is the analysis of a scientific theory as a set of inferentially related statements. A few of these statements serve as basic axioms or postulates from which other statements, termed scientific laws, are derived. These laws in turn are related in very complex ways to phenomena that we as human beings can observe fairly directly'.

The view that the deductive-nomological model originates with the logical positivists seems to be a grievous misunderstanding. The model seems to have originated with Popper (1968: p. 59, his italics, originally published in German in 1935), 'To give a *causal explanation* of an event means to deduce a statement which describes it [the *explanandum*], using as premises of the deduction one or more *universal laws*, together with certain singular statements, the *initial conditions*'. This idea was given more formal structure by Hempel & Oppenheim (1948), as presented in the preceding section [it is sometimes referred to as the Popper-Hempel model (Niiniluoto, 1995)]. Unfortunately, the Hempel–Oppenheim deductive-nomological model has been generalized into the covering-law model, which includes four types of explanation: deductive-universal (i.e. D-N), deductive-probabilistic, inductive-universal, and inductive-probabilistic (I-P) (Niiniluoto, 1995). As a Popperian I am uninterested in the last three forms of the covering-law model and will not comment on them further. The kind of explanation I am interested in pursuing is that described by the quote from Popper at the beginning of this paragraph, which corresponds to the deductive-nomological form of the covering-law model, which in turn corresponds to the explicitly stated method of physical scientists (Newton, 1729; Einstein, 1954; Bronowski, 1965; Feynman, 1965; Lederman & Teresi, 1993).

(4) Descriptive versus explanatory laws

Descriptive, empirical, or existential laws should be distinguished from explanatory laws. This is not always done, even by Popper's few avid supporters (Magee, 1973, 1997; Ereshefsky, 1991), and leads to unnecessary confusion. For example, 'water boils at 100 °C' could be considered a physical law. This is a descriptive law and in fact is a definition, the 100 degree point on the Celsius scale being the temperature at which fresh water boils in an open vessel at sea level. If we should boil fresh water in an open vessel at sea level, and should the thermometer read 99°, we would assume that the thermometer was miscalibrated rather than that the law was refuted.

Boyle's Law – the volume of a gas is inversely proportional to its pressure at a constant temperature – was a descriptive law when first discovered by Boyle and could be falsified directly by experiment and verificationist principles. We could experiment with air, oxygen, hydrogen, and helium, and then generalize the law to all gases – the method of induction. We test the generalization by experimenting with other gases. Nevertheless, as an inductive law, we cannot logically know that the law applies to all gases. Furthermore, Boyle's Law does not explain why gases behave as the law asserts.

Bernoulli later deduced Boyle's Law from Newton's Second Law and the further assumption that gases were particulate in nature (Rothman, 1995). Boyle's Law is another example of a descriptive law being subsumed by axiomatic explanatory laws, as Kepler's laws were earlier subsumed by Newton's laws. We say that Newton's Laws are explanatory because we now have an explanation for Boyle's Law, as well as for Kepler's Laws and much else.

Descriptive laws have limited applicability. From Boyle's Law we can predict only that we expect an unstudied gas's volume to be inversely related to its pressure. By contrast, Newton's Laws were widely applicable. Newton was able to predict planetary orbits, the shape of the earth, the acceleration of bodies near the earth's surface, the number of tides, and much, much more.

Universal explanatory laws, such as Newton's Laws, answer 'why' questions rather than 'what is' questions. They are usually statements that cannot be verified by direct observation. Inertia and gravitation are unobservables. How can we know that the hypothetical unobservables are responsible for what we observe without deducing some consequences and comparing them with evidence? In

biology, natural selection is a theoretical unobservable. What we see are its consequences. How can we know that natural selection is responsible for what we see without deducing some consequences and comparing them with evidence? The point of Popper's philosophy is that we cannot.

Descriptive laws and explanatory laws have different origins and a different logic – observation and induction in the former, imagination and deduction in the latter. If we lump all laws together and think that we are discussing the logic of explanatory laws when we are discussing that of descriptive laws, confusion is likely to follow. For example, consider the example of a stick and its shadow, which involves the laws of light transmission (Bromberger, 1966; Thompson, 1989; Sober, 1993). The height of a stick placed vertically in the ground can be predicted from the length of its shadow. We, however, would not say that the height of the stick was caused by the length of its shadow. In this neat example, explanation is separated from prediction, and, thus, seemingly we are allowed to have hypotheses that explain but do not predict. According to some biologists and philosophers of biology, then, natural selection is a perfectly good explanation even though predictions cannot be deduced from it.

The stick and shadow example shows only that explanation and prediction are not closely tied in some simple situations. For example, we do not need to know the physical laws of light transmission to predict the height of the stick from its shadow. All we need to know is some simple trigonometry. We do not need to know the laws in order to distinguish cause from effect, which is a matter of simple observation. On the other hand, we not only need to know but we must actively use Newton's laws in order to predict from initial conditions the motions of the planets and comets, the acceleration of a body, the shape of the earth, and so on.

(5) Syntactic versus semantic structure of theory

The deductive-nomological structure of theory (Hempel & Oppenheim, 1948; Hempel, 1965, 1966) has been subjected to much criticism (Dray, 1957; Scriven, 1959; Putnam, 1962; Bromberger, 1966; van der Steen, 1971; Suppe, 1972; Lloyd, 1988; Thompson, 1989; Gasper, 1991; Kitcher, 1991). I cannot, however, imagine another way of framing a deductive argument. In a syntactic theory, we state a set of universal laws and a set of conditions under

which those laws are said to apply, and then deduce the consequences of the laws in the stated conditions. The deduction, if a singular statement, is either empirically true or false. How else could we structure the argument?

Beatty (1981, 1987), Lloyd (1988), and Thompson (1989) seem to have offered an alternative – the semantic structure of theory. Newton's theory, as presented in Section V, is said to be 'syntactic'. Those favouring a semantic structure contend, quite correctly, that any syntactic theory (including Newton's) is incomplete because not all of its fundamental assumptions are spelled out. According to Thompson (1989: p. 55), for example, the Hardy–Weinberg law 'requires that one assume the axioms of arithmetic, mathematical logic, and Boolean algebra – none of which are [*sic*] among the theorems of the theory'. The Hardy–Weinberg law, however, is not wrong because these background assumptions are unstated. Scientists begin with an abundance of information that is, rightly or wrongly, taken for granted. Once we learn how to add and subtract, multiply and divide, we have little interest in stating the rules of arithmetic, assuming that we even know them formally, each time we propose or test a theory. I doubt that biologists would be interested in discussing the laws of optics when interpreting their observations made through microscopes or telescopes. Of course, one day a scientist or philosopher may explore the unstated assumptions and show that a theory, in violating one or more of them, makes predictions that are refuted by empirical fact.

Thompson (1989) makes the more important point that both Ruse (1973), who argued that the axiomatic structure of population genetics was the core of evolutionary theory, and Williams (1970, 1973), who argued for an axiomatic structure of selection theory (ignoring genetics altogether), distorted evolutionary theory in order to axiomatize it. He suggests [as do Beatty (1981, 1987) and Lloyd (1988)] that evolutionary theory is better understood as a family of interacting theories, which was best represented by a semantic account. The semantic conception offers 'a way of formalizing theories of physics and evolutionary theory that does not involve distortion and that avoids the undesirable features of the syntactic conception' (Thompson, 1989: p. 95).

The problem with the semantic version of evolutionary theory is that in combining two supposed syntactic theories (Ruse's population genetics and Williams's selection), neither of which predicts why

a fly has red eyes, a cheetah has spots, or an albatross has a one-egg clutch (or any other biological fact), we have one semantic theory that makes no predictions that can be verified or refuted by empirical fact. The semantic conception of evolutionary theory certainly provides explanations [often *ad hoc* hypotheses alleging the selection environment leading to the evolution of a trait (some examples in Tables 1–3)] for why a fly has red eyes, a cheetah has spots, or an albatross has a one-egg clutch (or virtually any other biological fact), but how do we know that these explanations are correct? That is for me the scientific and philosophical problem. How can we be confident in our explanations if, with our theory, we are unable to predict anything? If we cannot predict anything from our explanatory theory, how can we test it? An explanatory theory that makes no testable predictions (other than of the facts it was designed to explain) is little more than a fairy tale.

(6) Philosophy and biology

The view that Popper's philosophy, the Hempel–Oppenheim deductive-nomological structure of theory, and the received view are aspects of logical positivism or logical empiricism, even though untrue, seems sufficient reason for philosophers to disregard them. This mistaken view lies at the heart of the discussion of the philosophy of the biological sciences. Physicists can safely ignore the discussions and concerns of philosophers because their methods are established in tradition and have been passed on from generation to generation. Physicists have confidence in their theories because they work. If philosophers should challenge their theories about unobservable forces and particles, physicists will put a man on the moon or blow up a city with a single bomb. Biologists, however, cannot ignore philosophy because their tradition is Baconian induction, which, as far as I can tell, is not seriously challenged. Biologists mistakenly believe that they are applying deductive methods and that they have not been as successful at this as physicists because biological systems are more complex than physical systems. A shift from the verificationist philosophy of biology to a falsificationist philosophy in appropriate contexts will require biologists to discuss the philosophical basis of their hypotheses.

At the very least, biologists should be able to distinguish inductive generalizations from deductive theory, verificationism from falsificationism, and assumptions from predictions. For example, I pro-

posed a hypothetico-deductive theory explaining the pattern of interspecific territorial behaviour in birds and other animals (Murray, 1971, 1981). I made four assumptions, including, '(i) interspecific territoriality is territorial aggression directed toward members of other species that share similar features that stimulate intraspecific territorial aggression because of common ancestry, convergence, or accident,' from which I predicted that two species, which were interspecifically aggressive toward one another, should occupy different habitats or different geographic ranges, or they should eventually evolve differences in their territorial behaviour. These predictions were (and still are) consistent with the empirical evidence (Murray, 1971, 1981, in preparation). Nevertheless, Reed (1982) rejected my theory because he found that the great tit *Parus major* and the chaffinch *Fringilla coelebs* were interspecifically territorial on an island off the coast of Scotland. These species are so different in appearance that assumption (i) was inapplicable. He did not mention that his reported observations, that the larger and aggressively dominant chaffinches occupied hazel scrubland and the great tits occupied oak scrubland, a habitat that chaffinches did not enter, were facts that were consistent with the predictions.

Instead of concluding that the theory about the origins and consequences of interspecific territorial behaviour was wrong, Reed (1982) would have increased our understanding at the time by pointing out that interspecific territoriality had the ecological and behavioural consequences I attributed to it, *regardless* of its origin. The assumption about the similarity of appearance was an unnecessary initial condition. Reed (1982) did not recognize that his rejection of an initial condition of a deductive theory did not falsify the theory.

The most important philosophical insight (from my point of view) that Popper took from Hume (Magee, 1997) is his emphasis that the important *explanatory* laws of science could *never* be tested by verification. Furthermore, verification and falsification are not two sides of the same coin. A scientist interested in explanatory theory – that is explaining the observable in terms of the unobservable, such as the motions of planets in terms of inertia and gravitation or the traits of organisms in terms of natural selection – does not have a choice. He must be a falsificationist. A perfect example is inertial motion (discussed above), which is a product of the imagination, rather than an inference from observation, and it cannot be verified by reference to

observations (Einstein & Infeld, 1938). From it physicists must deduce singular statements that can be shown to be either true or false. The verification of *explananda* or of the *initial conditions* (depending on which was predicted) does not verify the laws.

Nevertheless, Popper is perhaps the most cited philosopher in the biological literature, if not all the literature of science during the past half-century. Biologists think they are following Popper's philosophy because they insist that hypotheses be 'testable'. Thus, the biological journals are full of titles that, following a colon, include some version of 'a test of hypotheses'. Biologists seem unaware that Popper (1979: p. 193, his italics) stated,

Only if we require that explanations shall make use of universal statements or laws of nature (supplemented by initial conditions) can we make progress towards realizing the idea of independent, or non-*ad hoc*, explanations. For, universal laws of nature *may* be statements with a rich content, so that *they may be independently tested* everywhere, and at all times. Thus, if they are used as explanations, they *may* not be *ad hoc* because they *may* allow us to interpret the [*explanandum*] as an instance of a reproducible effect. All this is only true, however, if we confine ourselves to universal laws which are testable, that is to say, falsifiable.

Instead of confining themselves to universal laws, biologists are constantly 'testing' *ad hoc* hypotheses by attempting to verify or falsify them by direct observation. I doubt that Popper would have suggested that the hypothesis, the 'size of a [female waterfowl's] lipid reserves is more likely to limit clutch size than is rate of protein ingestion' (Ankney *et al.*, 1991), could not be tested by verificationist principles. The hypothesis does not refer to unobservables and is limited to species of waterfowl. Rather, I think he would suggest that the hypothesis, 'the clutch size of birds has evolved by natural selection', could not be tested by verificationist principles because natural selection is an unobservable, theoretical entity. Ornithologists could be comfortable with one or another of their inductive hypotheses (Table 1), if their 100 tests or 1000 tests confirmed one of them, but their acceptance of an inductive generalization is psychological rather than logical. It is important to remember that Popper suggested that universal explanatory theories in science could not be tested by verificationist principles. Any further test of a universal explanatory theory can either falsify or not falsify it, but it can never verify it.

Thompson (1989: p. 24) asks, 'Is biology a

different kind of science than physics? and the corollary, Does biology conform to a logical empiricists [*sic*] conception of science?' There seems no consensus among philosophers on the answers to these questions (Beckner, 1968; Goudge, 1961; Smart, 1963; Manser, 1965; Ruse, 1973; Hull, 1974; Lloyd, 1988; Thompson, 1989). The answer to both questions is, 'that depends'. As practised, biology is a different kind of science from physics. Biologists violate every one of Newton's four rules of reasoning, which is one reason why they have failed to develop universal laws and predictive theory (Murray, 1992*a*). The logical structure of biology, however, *should not be* different from that of physics because logic transcends subject matter.

Does theoretical biology conform to the logical empiricist conception of science? I have not the slightest doubt that biologists are trained as verificationists (see Section III), but the quotations in Section II and in Section VII. 4, have led me to suggest that *theoretical* biology is not science at all (Murray, 1999*b*, 2000*a*). Furthermore, there seems no reason for biology to conform to the logical empiricist conception because logical positivism was refuted as a sound basis for theoretical, explanatory science seven decades ago (Popper, 1935).

(7) Discussion

As a theoretical scientist, I find all the philosophical side issues terribly distracting. The criticisms of the scientific method by philosophers do not affect how theoretical scientists should go about evaluating the correctness of scientific statements, such as Newton's laws. This may be why philosophers are held in such little regard by Nobel Prize-winning scientists (Feynman, 1995; Mullis, 1998).

Perhaps, as an outsider, I am puzzled by the apparently contradictory statements of philosophers because 'philosophers are prone to scandalous carelessness in transcribing quotations and to inaccurate descriptions, not to mention some highly questionable interpretations' (Hull, 1989: p. 205; referring to the examples reported in Williams, 1975). Philosophers, of course, are not alone in this. The biologists most supportive of Popperian falsificationism are the numerical taxonomists, who completely misunderstand Popper's philosophy. For example, 'Unfortunately, the strategy of falsificationism provides us at most with only a very vague guide to evaluating methods. Popper's writings, for example, are primarily concerned with the justifi-

cation of particular scientific theories, such as the taxonomic hypothesis that spiders are more closely related to whipspiders than they are to scorpions' (Platnick, 1979: p. 539). Even a casual reading of Popper (1968, 1979, 1989) indicates that his falsificationism has to do with an explicit method of testing universal theories about unobservables, such as Newton's laws, rather than with hypotheses about relationships among taxa (Hull, 1989). I would prefer not to deal with the misreadings (for whatever reason) of Popper, none of which addresses how we evaluate universal statements about unobservables, statements that are incapable of verification. I would prefer not to deal with the merits and demerits of all the hypotheses in the biological marketplace (some examples are listed in Tables 1–3). I would rather build what I think is a better theory, deductive-nomological rather than *ad hoc*, and test its deduced predictions with empirical evidence.

From a theoretical scientist's point of view, Newton's theory is not wrong because it is put in the deductive-nomological form or because the theory does not explicitly state all of its axioms. It is 'wrong' because it cannot predict and, therefore, cannot explain the precession of Mercury's orbit. The issues raised by the philosophers – that the deductive-nomological model may not be universally applicable to all fields of study, or that certain explanations do not require being deduced from laws, or that the model is syntactic and an incomplete description of the theory, and so on – simply do not refute, or falsify, Newton's Theory of Motion, much less any other physical theory. Newton's theory was falsified by the motions of Mercury and other empirical facts. It was not falsified by philosophical arguments.

Let us now consider directly some specific biological explanations, which are prominent in discussions of the philosophy of biology, with regard to the received view.

VII. BIOLOGICAL THEORY

(1) Classical genetics

Although Mendelian genetics is sometimes discussed as an example of a deductive-nomological theory in biology (Ruse, 1973, 1981), I do not know of a biology textbook that presents it in this way, and Mendel did not present his theory in this way (an English translation of his 1865 paper appears in Sinnott, Dunn & Dobzhansky, 1958). Mendel stated

(in Sinnott *et al.*, 1958: p. 421), 'The object of the experiment was to observe the variations in the case of each pair of differentiating characters and to deduce the law according to which they appear in the successive generations'.

Nevertheless, it is possible to put Mendel's theory into deductive-nomological form (Ruse, 1973, 1981). Mendel's Law of Segregation states that factors (i.e. alleles) for traits, say red flowers, are unaffected by the presence of factors for alternative traits, say white flowers, in the same cell. Mendel's Law of Independent Assortment states that the factors (i.e. genes) of different characters, say flower colour and pod colour, are inherited at random with respect to each other (because, as Mendel did not know, they are located on nonhomologous chromosomes). We can postulate further subsidiary hypotheses: each individual has two factors (i.e. alleles, symbolized, e.g. Y and y) for each characteristic (e.g. pod colour), one inherited from its female parent, the other from the male parent; one of the two alternative traits of a character is dominant (e.g. green pods) to the other (the recessive; yellow pods), that is, it is expressed even when only one allele for the trait is present. Thus, the genotypes for green pods are YY and Yy and that for yellow pods is yy; those for red flowers are WW and Ww and that for white flowers is ww. Without our belabouring the argument too much, if two double heterozygotes (YyWw) were crossed, we would predict that the phenotypic ratio of offspring should be nine plants with green pods and red flowers, three with green pods and white flowers, three with yellow pods and red flowers, and one with yellow pods and white flowers. We would predict that the genotype ratio would be 1 (YYWW): 2 (YYWw): 2 (YyWW): 4 (YyWw): 1 (YYww): 2 (Yyww): 1 (yyWW): 2 (yyWw): 1 (yyww). Many experiments confirm these predictions. Even more do not, mainly because other initial conditions affect the predictions, such as genes may be located on the same chromosome (linked), homologous chromosomes may exchange material (cross over), different genes may interact (epistasis), and so on. Nevertheless, an understanding of Mendel's Laws was essential for biologists to develop genetics beyond Mendel.

Although Mendel claimed that he 'deduced' his laws from his experiments, this hardly seems likely. Genes are unobservable, and their existence required some imagination. I suspect that he really did imagine the nature of inheritance and took a good guess at the laws, but then he wrote up his work in the inductive style so characteristic of biologists.

(2) Population genetics

Ruse (1973, 1981) cites the Hardy–Weinberg ‘law’ (sometimes referred to by biologists as a ‘theorem’, ‘principle’, or ‘rule’) as evidence showing that the structure of biological theory is like that of physical theory. Assuming that populations are infinitely large, that individuals mate randomly, that mutations do not occur, that selection does not occur, and that we limit consideration to two alleles at a single locus, then, according to the Hardy–Weinberg law, if the ratio of allele A to allele a is $p:q$ (where $p+q=1$), then the ratio of the genotypes AA, Aa, and aa in the population is $p^2:2pq:q^2$ (where $p^2+2pq+q^2=1$) and will remain so indefinitely. Inasmuch as evolution is usually thought of, ultimately, as a change in genotype frequencies over time, then a Hardy–Weinberg population is not evolving.

The Hardy–Weinberg law can hardly be considered to be Popperian or in the deductive-nomological form by any stretch of the imagination. Its assumptions are false: populations are small (certainly with respect to infinite size), individuals do not mate randomly (potential mates are choosy), mutations occur, selection occurs (genotypes have different survivorship schedules), and many genes exhibit multiple alleles. Worse, the deduction is contrary to what needs explaining (the changing frequencies of phenotypes).

We may be led by the Hardy–Weinberg argument to infer the reverse argument, as suggested by Freeman & Herron (1998: p. 128): ‘Hardy and Weinberg’s analysis identifies an explicit set of conditions under which populations will not evolve. It therefore also identifies an explicit set of forces that can cause evolution’. Explicitly, ‘it is predicted that *if* there are variations, *if* these are inherited, *if* one variant is more suited to some task than another, and *if* the success in accomplishing that task affects the ability of the organisms to survive in whatever happens to be their environment, *then* natural selection will produce an evolutionary change’ (Ghiselin, 1983: p. 65, his italics). This is the essence of the neo-Darwinian theory of evolution by natural selection. The fundamental problem is that there is no falsifiable prediction, that is a singular statement that could be found to be true or false.

(3) Molecular genetics

Perhaps the most physical of the biological sciences is molecular genetics. Watson & Crick (1953) proposed an elegant model for the structure of the

DNA molecule, a major component of chromosomes and thought by some, perhaps many, at the time to be the gene itself. Watson (1968) is unabashed in describing his guesses, all but one of which were demolished by Crick, who compared Watson’s guesses against his own knowledge of physico-chemical theory. The Watson–Crick model of the DNA molecule is nothing more than an *ad hoc* hypothesis, even if it was a bold guess that completely changed the field of genetics and all of biology. The structure of the DNA molecule was not deduced from the laws of physics and chemistry. The DNA molecule does not serve as a universal law from which further biological facts may be deduced (although it certainly eliminated many possibilities). None of this, I hasten to add, detracts from the importance of the DNA molecule for understanding biology. The discovery of DNA’s molecular structure is a preeminent example of a theoretical contribution to biology that is not in the form of a deductive-nomological argument. Not all progress in science necessarily comes from the application of Popper’s philosophy. This does not mean that deductive-nomological theory should not be used in biology.

(4) Population dynamics

Ecologists know that populations (groups of individuals of the same species within a circumscribed area) fluctuate in size from year to year and that over the span of many years the mean growth rate is zero (except for species on the road to extinction). An ecological problem has been to explain why populations fluctuate within an upper and lower boundary and have a long-term growth rate of zero. Explanations divided into two broad classes, the density-dependent regulation hypotheses (DDRHs), the chief proponents of which were Nicholson (1933, 1954, 1958), Solomon (1949, 1957, 1964, 1969), Lack (1954, 1966), and Huffaker (1958), and the population limitation hypotheses (PLHs), the chief proponents of which were Thompson (1939, 1956), Andrewartha & Birch (1954, 1960), den Boer (1968), and Reddingius (1971). The proponents of the DDRHs seem to have prevailed, judging from the number of DDRH supporters (e.g. Royama, 1977, 1992; Sinclair, 1989; Lawton, 1992; Murdoch, 1994; Berryman, 1997; Turchin, 1995, 1999) and the fact that DDRHs are treated in detail in virtually every ecology textbook.

DDRHs have been favoured by ecologists despite the great difficulty ecologists have in finding evidence of the alleged density-induced negative feed-

back loops (Turchin, 1990; Greenwood & Baillie, 1991; Woiwod & Hanski, 1992; Murdoch, 1994). What is more telling is the philosophical attitude of at least several of the prominent proponents of density dependence:

(1) ‘... the absence of field evidence does not, and will not, make the advocates of density-dependent regulation change their minds ... because, given certain assumptions about the persistence of natural populations, the existence of density-dependent regulation becomes a logical necessity’ (Lack, 1966: p. 291);

(2) ‘The concept of density-dependent regulation ... is derived through pure logical deduction from one major premise, namely the persistence of populations in the wide sense. It is knowledge obtained a priori. There is no need to test its validity against observations ...’ (Royama, 1977: p. 33);

(3) ‘Royama (1977) has argued convincingly that tests for density-dependence are unnecessary’ (Berryman, 1991: p. 142); and

(4) ‘... density dependence is a research program, a theoretical framework with which to investigate the causal factors of population fluctuations, not a hypothesis to be falsified or corroborated’ (Turchin, 1999: p. 157).

The notion that evidence is unnecessary is dogma, not science. DDRHs are guesses without supporting evidence (Murray, 1979, 1982, 1994*b*, 1999*a*, *b*, 2000*a*, 2000*b*).

(5) The theory of natural selection

The central principle of biology is the theory of evolution by natural selection, first proposed by Darwin and Wallace in 1858 and greatly elaborated in the 1930s and 1940s by scientists such as T. Dobzhansky, J. S. Huxley, E. Mayr, B. Rensch, G. G. Simpson, and G. L. Stebbins (Mayr, 1982). Despite its importance as a unifying principle *explaining* observations in paleontology, embryology, development, anatomy, physiology, genetics, behaviour, ecology, and so on, its scientific status has been frequently challenged (Scriven, 1959; Goudge, 1961; Manser, 1965; Beckner, 1968; Popper, 1978, 1979; Thompson, 1989), mainly on the grounds of its being tautologous and its failing to produce testable predictions. Several biologists and philosophers have mounted a spirited defence of its scientific status (Ruse, 1973, 1981; Mayr, 1982, 1988, 1991, 1996; Futuyma, 1983; Naylor & Handford, 1985). Most simply assume it to be true,

even though it suffers from some truly fundamental problems.

(a) *The tautology problem*

A tautology is a sentence that is true because of its logical form (Corcoran, 1995). The sentence, ‘It is the case that swans are white, or they are not white’ (i.e. P or not- P) is a tautology. We know that it is true even if we do not know the meaning of ‘swans’ and ‘white’. The sentence, ‘All cats are cats’, is also a logical tautology. We do not need to know the meaning of ‘cats’ to know that the sentence is true. Not all true sentences, however, are logical tautologies. For example, ‘two plus two equals four’ is a true statement (at least in everyday arithmetic). Nevertheless, we must know the meanings of ‘two’, ‘four’, ‘plus’, and ‘equals’ in order to conclude that it is a true statement. Definitions of words are true statements, although their truth is an agreed-upon convention. What we should avoid in science are hypotheses that are logical tautologies. We cannot avoid the true statements of mathematics, but we should be careful to use words in the same way if we are to argue about the processes to which they apply.

A major problem for evolutionary theory has been Herbert Spencer’s phrase, ‘survival of the fittest’, which is supposed to describe the evolutionary process. According to Popper (1979: pp. 241–242, his italics), ‘... the trouble about evolutionary *theory* is its tautological, or almost tautological, character ... there does not seem much difference, if any, between the assertion “those that survive are the fittest” and the tautology “those that survive are those that survive.” For we have, I am afraid, no other criterion of fitness than actual survival, so that we conclude from the fact that some organisms have survived that they were the fittest, or those best adapted to the conditions of life’, an argument also advanced by Smart (1963). Popper suggested that the theory must be restated in a less vague way.

I am astonished that biologists (Peters, 1976, 1978, 1991; Ferguson, 1976; Caplan, 1977; Castrodeza, 1977; Stebbins, 1977; Mayr, 1982, 1988; Riddiford & Penny, 1984) and philosophers of biology (Ruse, 1973, 1977, 1981; Hull, 1974; Mills & Beatty, 1979; Sober, 1984, 1993) are discussing whether ‘survival of the fittest’ is a tautology or not because for at least fifty years an alternative concept has been that ‘natural selection is differential reproduction’ (Simpson, 1949: p. 258). Nevertheless, this alternative statement does not resolve the apparent tautology of evolutionary theory.

The important point to make is that neither 'survival of the fittest' nor 'differential reproduction' has produced predictions that are testable with independent evidence. What is needed is a statement that allows us to deduce independently testable predictions. This problem leads us to the problem of defining fitness.

(b) *The fitness problem*

According to Stearns (1976: p. 4), fitness is 'something everyone understands but no one can define precisely', a view seconded by Mayr (1988) and de Jong (1994). There seems to be no consensus on what it is, how to define it, and how to measure it by either biologists or philosophers (e.g. Fisher, 1930; Kimura, 1956, 1958; Williams, 1966; Denniston, 1978; Mills & Beatty, 1979; Rosenberg, 1982, 1991; Brandon & Beatty, 1984; Nur, 1984, 1987; Sober, 1984; Murray, 1985*b*, 1990, 1997; Rosenberg & Williams, 1985, 1986; Endler, 1986; Byerly & Michod, 1991*a, b*; da Cunha, 1991; Ettinger, Jablonka & Falk, 1991; Kleiner, 1991; Lennox, 1991; Maynard Smith, 1991; Ollason, 1991). Biologists and philosophers are unable to define fitness precisely because their conception of natural selection is too vague. The problem is that natural selection is an inherently quantitative process, which biologists and philosophers are trying to understand without resorting to mathematics (much less requiring that it lead to deducible consequences).

The problem of this undefined or vaguely defined fundamental term is compounded by the unit of selection problem.

(c) *The unit of selection problem*

Without an explicit definition of fitness, we are left with the problem of determining what is supposed to be fit. Is the unit or target of selection the gene, individual, family, population, community, or even ecosystem (Wynne-Edwards, 1962; Hamilton, 1964; Lack, 1966; Williams, 1966; Lewontin, 1970; West Eberhard, 1975; Wilson, 1975; Dawkins, 1976; Alexander, 1979; Hull, 1980)? Do we explain biological diversity as resulting from gene selection, natural selection, kin selection, group selection, community selection, or one of them, or all of them, or some combination at some time or other?

We cannot really answer this question, especially if we do not require that whatever statement we come up with must be part of some deductive system that produces empirically testable predictions.

I agree with Popper (1978, 1979) that the theory of evolution, as it is presently understood, is a metaphysical research program simply because there are no recognized laws that allow prediction of any biological facts. The theory of natural selection, instead, is a framework that allows the proposal of testable hypotheses about evolution.

(d) *A proposed solution to these problems*

Let us begin with what we are trying to explain. What is the problem? At a minimum, evolution refers to the changes that we are able to observe in the physical appearance (the phenotypes) of plants and animals, changes that have been documented in the fossil record. We want to explain how the appearance of individuals within a population changes over the course of time. What do we know that may serve as clues? The individuals of contemporaneous populations of plants and animals differ in their appearance. For example, some have red eyes, others have white eyes. From much experimental work, we know that some of these phenotypic differences reflect underlying genotypic differences, whereas others reflect differences in the environments of the developing individuals. For example, if we chop the tails off a strain of long-tailed mice and off another strain of short-tailed mice, making them 'no-tailed', the offspring of the former will be long-tailed and those of the latter will be short-tailed. The offspring of the no-tailed mice will be either long-tailed or short-tailed. We cross the long-tailed and short-tailed mice in Mendelian experiments and show that the difference between the two strains is a result of genetic differences. We know, then, that only those phenotypic traits having a genetic basis can be passed on to the next generation and, thus, are subject to selection.

Mathematically, if these traits and their genotypes are associated with differences in the possessors' probabilities of surviving and breeding, then the traits and genotypes will increase or decrease at different rates. It is the genotypes and traits that change in frequency over time, but these are brought about by differences in the survival and reproduction of the individuals possessing those genotypes and traits (Murray, 1990, 1995, 1997).

The implications of this description of the evolutionary process are that (1) the 'fitness' of a genotype or phenotype is best measured as the rate of change in the alternative genotypes or phenotypes of a population, often known as the Malthusian parameter (Fisher, 1930; Murray, 1979;

Charlesworth, 1980), but measured as described in Murray (1990, 1995, 1997), and (2) the unit of selection is best thought of as the individual organism because it is the possessor of the genotypes and phenotypes and it is what lives, reproduces, and dies. We may be distracted by the fitness of each individual in the population, as measured by his or her success in surviving and reproducing, and state that individual A is more fit than individual B. Individual fitness, however, does not tell us the evolutionary fate of any of an individual's traits. A red-eyed individual may have many offspring, and a white-eyed individual may have few, but the white genotype (*ww*) may increase more rapidly than the red genotypes (*WW*, *Ww*).

I simulated a population with complex genetic and demographic structure (Murray, 1997). There were four phenotypes and nine genotypes (two alleles for each of two independent loci). I gave the four phenotypes and their associated genotypes different rates of age-specific survival and reproduction and showed that the genotype and phenotype that prevailed had neither the greatest survival nor the greatest fecundity. The relationship between reproduction, survival, and fitness is neither simple nor intuitive (Murray, 1990, 1995, 1997). Simple survival and reproduction of individuals provide the wrong clues.

Instead of characterizing evolution as 'survival of the fittest' or as 'differential reproduction', I proposed a First Law of Evolution (see below). No doubt, others may propose alternative hypotheses and call them laws. Alternative theories should be evaluated by deducing the consequences of the laws and initial conditions and testing these by comparing them with empirical facts.

Before proposing a theory, I will next review some of what needs explaining with regard to the evolution of life-history traits, such as clutch or litter size, number of broods reared per year, life expectancy, lifetime reproductive success, mating relationships, and sexual size dimorphism.

VIII. LIFE HISTORY THEORY

David Lack, an ornithologist, reviewed the data on clutch size in birds (the number of eggs laid in a nest) and confirmed what was already known – that, for example, clutch size increased with increasing latitude (Lack, 1947, 1948*a*). He proposed that parent birds at high latitudes during the breeding season had more hours in their day to gather food for

their young and, thus, were able to rear more young than parent birds at lower latitudes could with shorter days. He generalized this argument to apply to all birds: '... clutch size is considered to be ultimately determined by the average maximum number of young for which the parents can find enough food' (Lack, 1947: p. 331). He quickly applied his hypothesis to mammals and reptiles (Lack, 1948*b*, 1954). Lack was consistent in interpreting clutch- and litter-size variations in terms of his universally applicable hypothesis throughout his life (Lack, 1966, 1968). Also, from his hypothesis and from his understanding of natural selection, he expected that the most successful clutch size should be the most frequent in a population (because it had been selected for). This expectation is contrary to evidence. The hypothesis is laden with problems and caveats: 'the normal clutch tends to be somewhat larger than the number of young that the parents can raise in an average year, the extra egg or eggs being a reserve that can be utilized in good years' (Lack, 1954: p. 41), 'The rate at which the nestlings grow might also influence the evolution of clutch-size, as the same quantity of food per day would allow the raising of a few young rapidly or more young slowly' (Lack, 1954: p. 41), and so on. His theory cannot predict the clutch size variations in birds.

Unexplained by Lack's hypothesis was the fact that the clutch sizes of nocturnal species, such as owls, increased with increasing latitude (von Haartman, 1971). This problem was 'solved' subsequently by an *ad hoc* saving hypothesis – that food is harder to find, even though more abundant, in the tropics than at higher latitudes (Owen, 1977).

Lack's method was to infer explanations from tables of comparative data, as revealed in his major books (Lack, 1954, 1966, 1968). As such, it was strongly Baconian. Lack's hypothesis was an extension of an inductive generalization. Biological understanding was simply to fall out of compiling long lists of comparative data. But, as Einstein noted 'intuitive conclusions based on immediate observation are not always to be trusted' Despite its problems (Murray, 1979, 1985*b*), Lack's hypothesis continues to receive favourable treatment (Godfray, Partridge & Harvey, 1991; Monaghan & Nager, 1997).

Lack's hypothesis on clutch size, however, was challenged as soon as it appeared. Skutch (1949), a tropical biologist, argued that whatever the merits of Lack's hypothesis for temperate species, his hypothesis was not applicable to tropical species.

Skutch (1949) proposed that the small size of clutches of tropical species was an adaptation that reduced the predation rate on the contents of nests. With Skutch, the biologists' explanation of clutch size becomes tautologous (i.e. P or not- P): that is, the clutch size reflects either (P) the number of eggs in the clutch that has been evolved to correspond with that from which, on average, most young are raised or (not- P) something else (such as the number of eggs that increases the probability of survival of eggs and young in the nest), except that one hypothesis was applicable to high-latitude species and the other to low-latitude species.

Subsequently, however, the 'something else' included more than a dozen hypotheses 'explaining' the evolution of clutch size in birds (Table 1). These are *ad hoc* hypotheses, none (other than Lack's hypothesis and Cody's version of it) was even intended to be universal. All of these, to be sure, are proposed under the umbrella of the theory of natural selection, but can they all be true?

With regard to the rather small matter of the synchronous and asynchronous hatching of birds' eggs, there are no fewer than 20 named hypotheses (Table 2), none intended to be universal by their proposers.

With regard to the evolution of mating systems (i.e. monogamous, polygynous, polyandrous, and polygynous-polyandrous relationships between the sexes), Emlen & Oring (1977) identified several categories: monogamy, resource defence polygyny, female (or harem) defence polygyny, male dominance polygyny (including explosive breeding assemblages and lekking behaviour), rapid multiple clutch polygamy, resource defence polyandry, male defence or 'harem' polyandry, and female access polyandry. Wittenberger (1979) recognized even more categories (Table 3). Many of these simply describe the social and ecological situation. I could discern no overriding hypothesis from which these categories could be deduced.

The males and females of a species often differ in size, males sometimes being larger, females sometimes being larger. We are again overwhelmed with *ad hoc* hypotheses. Mueller & Meyer (1985) discussed a nonexhaustive list of 14 hypotheses proposed to explain why female raptors (hawks and owls) are larger than the males. Research on sexual size dimorphism (SSD) in birds has focussed on raptorial birds, even though many other taxa show female-larger SSD and the Charadrii show an even greater diversity of pattern of SSD than raptors (Jehl & Murray, 1986).

Biologists and philosophers are agreed that the complexity of the biological world precludes the possibility that this diversity of *ad hoc* hypotheses (and I am only discussing birds here) could be explained by a few universal laws in combination with initial conditions. Are they justified in taking this position?

IX. A DEDUCTIVE THEORY OF LIFE HISTORY EVOLUTION

The only way to show that the methods of the physicists and Popper are useful in developing unifying, predictive, and explanatory theory in biology is to produce a unifying, predictive, and explanatory theory, which satisfactorily predicts a range of biological facts. The theory should explicitly state the laws [guesses, as Feynman (1965) and Popper (1989) characterize them], the initial conditions, the deduced predictions, and the confirming evidence. Remember, a theory does not explain everything. At this stage of the development of predictive theory in biology, we should be looking for a theory of universal laws that will predict anything. If we can discover such a theory, then we falsify the belief that such theories are impossible in biology. I am hopeful that my having shown that predictive theory in biology is possible will encourage other biologists to develop further theories in this and other areas of biology (Murray, 2000c).

The following discussion outlines the theory with minimum reference to the mathematics involved. Those readers interested in the mathematical arguments and deductions should see Murray (1979, 1984, 1985a, c, 1990, 1991a, b, 1992b, 1994a, 1995, 1997; Murray & Nolan, 1989; Murray, Fitzpatrick & Woolfenden, 1989). Let us begin with the laws (these have been treated in greater detail in Murray, 1999c, 2000c):

First law of evolution : *Genotypes and phenotypes with the greatest Malthusian parameter increase more rapidly than those with smaller Malthusian parameters.*

This law is another way of writing Darwin's Theory of Natural Selection, as it was modified by the evolutionary synthesis of the 1930s and 1940s (Mayr, 1982). This law refers to the following evolutionary process. Individuals in a population differ in their appearance (e.g. some have red eyes, others have white eyes). If these phenotypic differences reflect underlying genotypic differences, and if these traits are associated with differences in the possessors' probabilities of surviving and breed-

ing, then the traits and genotypes will increase or decrease at different rates. It is the genotypes and traits that change in frequency, but these are brought about by differences in the *probabilities* of survival and reproduction of the individuals possessing those genotypes and traits.

Written in this way, the law allows for mathematical treatment and quantitative prediction. If we could determine the probabilities of age-specific survival and fecundity for each genotype or phenotype, we could calculate the rate of change of a genotype (m) or a phenotype (ρ), what has been called the Malthusian parameter (Fisher, 1930; Murray, 1979, 1997; Charlesworth, 1980), with

$$1 = \sum \lambda_x \mu_x e^{-rx}, \quad (1)$$

where r represents m for genotypes or ρ for phenotypes (depending on the kind of input data that is available), λ_x is the probability of individuals (either males or females) of a specific genotype or phenotype surviving from birth (in live-bearing animals) or from being laid as an egg (in egg-laying animals) to age class x , μ_x is the mean apparent fecundity of individuals (either males or females) of that genotype or phenotype and age class x , and e is the base of the natural logarithms (see Murray, 1990, 1995, 1997, for fuller treatment of the method).

Second law of evolution : *In the absence of changes in selection forces, a population will reach and remain in an evolutionary steady state.*

A population is in an evolutionary steady state when m for a particular genotype and ρ for its associated phenotype are zero. Ecologically, a population's size fluctuates between upper and lower bounds and has a long-term growth rate (r in equation 1, combining all genotypes) of zero.

Third law of evolution : *Selection favours those females that lay as few eggs or bear as few young as are consistent with replacement because they have the highest probability of surviving to breed again, their young have the highest probability of surviving to breed, or both.*

This law is contrary to the conventional wisdom [a collection of *ad hoc* hypotheses (Table 1)] of biologists studying the evolution of life-history traits and especially the evolution of clutch size (as recounted above). The hypothetical laws should be evaluated on how well they lead to predictions of fecundity variations in plants and animals rather than on whether they are consistent with the

conventional wisdom. I have discussed various explicit predictions regarding clutch size in birds and their supporting evidence (Murray, 1979, 1985a, 1991b). Here I will discuss only two.

Laws 1 and 2 allow us to write an equation relating various life-history parameters (Murray & Nolan, 1989), that is,

$$C = \frac{a+1}{\frac{\omega}{\alpha} \frac{1}{\sum_x \lambda_x \sum_i P_i}}, \quad (2)$$

where C is mean clutch size, a is the primary male/female sex ratio (assumed to be 1 in birds), λ_x is the probability of surviving from birth (in birds, from the laying of the egg) to age class x (of those individuals from successful clutches or litters), α is the average age class of first breeding, ω is the age class of last breeding, P_i is the probability of rearing brood i ($i = 1, 2, 3, \dots$), and $\sum_i P_i$ is the mean number of broods reared. Note that $\sum_i P_i = \sum_i c_i s_i$, where c_i is the number of brood- i clutches and s_i is the probability that a brood- i clutch produces any young to leave the nest (Murray, 1991a, b).

Equation (2) accurately predicted the clutch size of the prairie warbler *Dendroica discolor* (Murray & Nolan, 1989), the Florida scrub jay *Aphelocoma coerulescens* (Murray *et al.*, 1989), and the house wren *Troglodytes aedon* (Kennedy, 1991), showing that no important parameter had been overlooked. Furthermore, according to Wootton, Young & Winkler (1991), equation (2) must be true, and I agree with them (Murray, 1992b). This equation must hold, whether one accepts Lack's hypothesis, Skutch's hypothesis, my hypothesis, or some other hypothesis as the best explanation for the evolution of clutch size. We may ask, then, what does equation (2) tell us about how environmental factors affect or constrain the evolution of clutch size and other life history traits of a population?

From equation (2), clutch size should be larger in species that have larger primary male/female sex ratios, greater juvenile or adult mortality rates (smaller $\sum_x \lambda_x$), later age of first breeding (smaller $\sum_x \lambda_x$), or smaller number of broods reared (smaller $\sum_i P_i$).

This equation allows us to make specific predictions about the life histories of organisms, which we may then compare with the empirical facts.

Proponents of the semantic view of theory structure will point out that these three laws do not represent all the assumptions of the theory. In addition to the rules of arithmetic, Law 1 assumes

Mendel's laws of inheritance, the occurrence of mutation and selection, and so on. The semanticists are absolutely correct. A philosopher may be interested in determining all of the assumptions of the theory. I think the unstated assumptions will prove to be noncontroversial. One should note that my not stating all the assumptions does not make the theory wrong. Only a flaw in the logic or an empirical test refuting a prediction can determine the theory to be wrong.

(1) Evolution of clutch size in birds

Birds lay no more than one egg per day. Thus, it takes longer to lay a big clutch than a small clutch. If the probability of a nest's contents surviving from one day to the next is less than 1, then the probability that a clutch will produce any young to leave the nest (s_i) should be greater for a smaller clutch than for a larger clutch (Murray, 1991*a, b*, 1999*c*). Furthermore, in some finite period of time, the females of a genotype for a smaller clutch are likely to be able to lay more replacement clutches following failures (increasing c_i). Thus, the probability of rearing a brood- i clutch ($P_i = c_i s_i$) is greater for a smaller clutch, presumably increasing the number of broods reared by the females of a genotype ($\sum_1^n P_i$). Also, in some finite period of time, the females of a genotype for a smaller clutch are likely to be able to rear a second brood following a first brood success. From these assumptions, selection should favour a clutch size of 1, maximizing $\sum_1^n P_i$, but a clutch size of 1 may not produce enough young to balance mortality. Thus, the minimum clutch size cannot be smaller than the replacement number. The hypothesis (Law 3) is that clutches greater than the replacement clutch size reduce c_i and s_i for brood- i clutches and, thus, reduce $\sum_1^n P_i$.

The $\sum_x \lambda_x$ is the mean number of breeding seasons for the females of a genotype, and $\sum_1^n P_i$ is the mean number of broods reared per year. Thus, the lifetime reproductive success (in terms of number of broods reared) for females of a genotype is the product of the mean number of breeding seasons and the mean number of broods reared per female per breeding season, that is, $\sum_x \lambda_x \sum_1^n P_i$, the denominator on the right-hand side of equation (2). An implication of equation (2), then, is that there is an apparent trade-off between clutch size and lifetime reproductive success, the greatest lifetime reproductive success occurring with the minimum clutch size consistent with replacement. If this is a trade-off, however, it is a trade-off without options.

This is the rationale for Law 3, which, however, as an axiom, does not require direct justification.

Now, suppose that $\sum_1^n P_i$ is directly correlated with the length of the breeding season because where breeding seasons are long females are able to produce more replacement clutches following clutch failure and are able to rear more than one brood per year than females living where breeding seasons are short. The prediction is that, because $\sum_1^n P_i$ is greater where breeding seasons are longer, the clutch size should be smaller where breeding seasons are longer. This is a relationship unknown to ornithologists but predicted by me (Murray, 1979, 1985*a*, 1991*b*). The prediction is confirmed by clutch size being smaller at tropical latitudes than at higher latitudes (Lack, 1947, 1948*a*, 1954, 1968; Cody, 1966, 1971; Klomp, 1970; Skutch, 1985) and smaller in the southern hemisphere than in the northern (Moreau, 1944; Yom-Tov, 1987; Rowley & Russell, 1991; Yom-Tov, Christie & Iglesias, 1994) because breeding seasons are longer in the tropics than at higher latitudes and at southern latitudes than at comparable northern latitudes (Baker, 1938; Skutch, 1950; Wyndham, 1986; Rowley & Russell, 1991; and Yom-Tov *et al.*, 1994). It is confirmed further by clutches being larger in species with short breeding seasons within the tropics (Marchant, 1960; Sargent, 1993). I have reviewed the evidence in greater detail elsewhere (Murray, in preparation). Here, we have a prediction of an empirical relationship that was unrecognized by ornithologists before the prediction was made, and the prediction (so far) is consistent with empirical evidence.

Second, suppose that $\sum_1^n P_i$ is inversely correlated with the intensity of predation, being smaller where predation is greater, because predation on nest contents reduces s_i for each brood- i clutch and, thus, $\sum_1^n P_i$. (Of course, c_i may increase.) This prediction is contrary to conventional wisdom, otherwise known as the nest-predation hypothesis (Skutch, 1949; Perrins, 1977; Slagsvold, 1982; Martin, 1992). Direct data are scarce. In the only comparative study of which I am aware, Martin (1988) reported that both predation rate on nest contents and clutch size were greater in ground-nesting species than in above-ground-nesting species of New World warblers (Emberizidae: Parulidae), consistent with the prediction of my theory and contrary to the nest-predation hypothesis.

The theory also explains (Murray, 1979, 1985*a*, 1991*b*) the increasing clutch size of nocturnal species with increasing latitude (von Haartman, 1971), which is not otherwise explained, except by an *ad hoc*

hypothesis saving Lack's hypothesis (Owen, 1977). It explains the large clutch sizes of short-lived cavity-nesting birds (Newton, 1989), and the universal clutch size of one egg in all procellariiform birds (Lack, 1968). The full scope of the theory awaits further study.

(2) Evolution of hatching pattern

As noted, birds lay no more than one egg per day. Incubation may begin with the laying of any egg in the sequence. Thus, in some species eggs hatch at the same time, synchronously, and in other species eggs hatch on different days, asynchronously. Stoleson & Beissinger (1995) and Slagsvold, Amundsen & Dale (1995) have identified 20 named hypotheses that have been proposed to explain asynchronous hatching patterns in birds (Table 2). None was intended to be a universal hypothesis.

According to theory (Murray, 1994a, 1999c), the 'nest failure hypothesis' of Tyrväinen (1969), Hussell (1972), and Clark & Wilson (1981) could be applied universally, because early incubation and asynchronous hatching increase the probability that any young will leave a nest, increasing s_i and, thus, $\sum_1^n P_i$ at the cost of reducing the number of young that actually leave an individual nest (Murray, 1994a, 1999c). Some individuals of the brood are ready to leave a nest before their nestmates are ready, should a predator or inclement weather intrude before all nestlings are ready to leave the nest. It is better to rear some young from a clutch than lose them all by trying to rear them all by starting incubation with the last egg. In species in which all young leave the nest at or shortly after hatching, however, incubation should start with the last egg and hatching of all eggs should occur at about the same time. Early incubation and asynchronous hatching in species with precocial young would increase the probability of losing the young that had not hatched by the time the earlier hatched young were leaving the nest.

The brood reduction hypothesis, often thought to explain asynchronous hatching (Lack, 1954, 1966), is the notion that the loss of later hatched young (through starvation or siblicide) allows parents to adjust their brood size to the available food supply. According to my theory, brood reduction seems to be an adaptation that allows parents to rear as many young from a successful brood as they can, increasing $\sum_x \lambda_x$, by increasing the probability of survival of the survivors at the cost of reducing the potential maximum number of young from a clutch. The insurance hypothesis, which is the notion that

females lay more eggs than necessary as a means of assuring some of the young to survive, is built into Law 3 and equation (2). According to Law 3 females lay as many eggs as are necessary to assure replacement, regardless of which egg or young in a sequence succumbs. Several of the other hypotheses are coincidental consequences of selection maximizing $\sum_x \lambda_x \sum_1^n P_i$, rather than specific adaptations (Murray, 1994a, 1999c).

(3) Evolution of mating systems

The mating relationships of the individuals of a population are monogamy [one male-one female mated during a particular breeding episode (from courtship to independent young)], polygyny (one male mated to two or more females with overlapping breeding episodes), polyandry (one female mated to two or more males with overlapping breeding episodes), and polygyny-polyandry (males and females having two or more mates with overlapping breeding episodes). A dozen or so *ad hoc* hypotheses (Table 3) have been proposed to explain the evolution of mating systems (Wilson, 1975; Emlen & Oring, 1977; Wittenberger, 1979; Oring, 1982). An alternative explanation follows from my clutch-size theory (Murray, 1984, 1985c).

We have seen above (equation (2)) that the clutch size of a genotype (C) is a function of its possessors' probabilities of surviving to different ages x (λ_x), age of first breeding (α), age of last breeding (ω), and probabilities of rearing one, two, or more broods (P_1, P_2, \dots, P_n). The hypothesis is that selection maximizes $\sum_x \lambda_x \sum_1^n P_i$ by minimizing clutch size.

Suppose that, because of the territorial behaviour of males or because of differences in survival of males and females, only 10 males establish territories in a habitat suitable for breeding, and that there are 15 females ready to breed. Only 10 females have an opportunity to breed with a monogamous male. The other five may wait until an unmated male becomes available. If they wait until later in the breeding season, they reduce their probability of successfully breeding in that year (smaller $\sum_1^n P_i$ than those starting earlier). If they wait until a later year, the age of first breeding, α , is greater, decreasing $\sum_x \lambda_x$ and reducing $\sum_x \lambda_x \sum_1^n P_i$. The individuals with the genotype "wait" must have a greater annual fecundity throughout life (equation (2)). Instead, females may accept an already mated male (becoming part of a polygynous relationship). The cost to the genotype 'join already mated male' is often the loss of paternal assistance in rearing young and,

perhaps, a reduced $\sum_1^n P_i$ (but the genotype will have a greater $\sum_x \lambda_x$). Which genotype is selected depends on which combination gives the greatest m (equation (1)). A similar argument can be made for the evolution of polyandry (fewer females available for breeding than males ready to breed).

These considerations led me to propose a demographic theory for the evolution of mating systems (Murray, 1984). Polygyny and polyandry evolve when the theoretical replacement fecundity (μ_r) of females (eggs laid) and males (eggs fertilized) that wait is greater than the annual fecundity that they can expect from a monogamous relationship (μ_m). Thus, polygyny evolves when $\mu_r > \mu_m$ for females; polyandry evolves when $\mu_r > \mu_m$ for males; polygynous–polyandrous relationships evolve when $\mu_r > \mu_m$ for both males and females; monogamy evolves when $\mu_r \leq \mu_m$ for both males and females. This theory is treated in detail elsewhere (see Murray, 1984, 1985c).

This theory seems consistent with the fragmentary evidence that is available (Murray, 1984). I have illustrated the theory with two examples (Murray, 1985c). Consider the prairie warbler *Dendroica discolor*. From its survivorship schedule (Nolan, 1978), we can calculate a theoretical replacement fecundity (μ_r), with $2/\sum_x \lambda_x$ (Murray, 1979, 1985a), for each age of first breeding (α). With breeding beginning at age two, it is 21 eggs in every year of reproductive life. Inasmuch as the average female actually lays 11 eggs in 3.2 clutches during a breeding season (Nolan, 1978), females should begin breeding at age one, which they do. Furthermore, at the beginning of the breeding season the females outnumbered the males on territory, and some males were polygynous (Nolan, 1978).

By contrast, from survivorship data on the Laysan albatross *Diomedea immutabilis* (Fisher, 1975), μ_r is < 1 for every age less than 16 years. It is not surprising, then, that the average age of first breeding of females of this species is 8.9 years, that birds skip breeding in some years, and that the mating system is monogamous (Fisher, 1975).

(4) Evolution of sexual size dimorphism

Males and females of most species differ in size. Sometimes males are the larger sex, and sometimes females are the larger sex. The problem of why one sex is larger than the other has been a subject of debate among evolutionary biologists since Darwin (1871). Again, there is an endless supply of *ad hoc* hypotheses available for the field biologist to choose

from for a ‘test’ (Mueller & Meyer, 1985; Jehl & Murray, 1986). The literature continues to be filled with such tests. Jehl & Murray (1986), however, proposed a hypothesis, which they claimed was applicable to all birds and some other animals. It is certainly not applicable to all species of animals. There are other (as yet unknown) initial conditions that lead to sexes of different size.

Jehl & Murray (1986) were confronted with explaining why species of birds with clutch sizes and mating relationships having evolved in the way described in the preceding sections evolved differences in size between the sexes. For example, why does one polygynous species have a male-larger dimorphism and another polygynous species have a female-larger dimorphism?

We accepted the initial condition that in flying animals, such as birds, selection for maneuverability during flight resulted in selection for smaller size (Andersson & Norberg, 1981). Thus, we hypothesized that female-larger dimorphism should occur in those species in which males evolved elaborate aerial, acrobatic courtship displays, males contested for territorial dominance in aerial combat, or both, and that male-larger dimorphism should occur in those species in which males evolved courtship and territorial behaviour that occurred on stationary surfaces (they may nevertheless have nonacrobatic flight displays). Female-larger dimorphism could evolve also when females were the territorial or courting sex. This resulted in 16 combinations of mating system and size dimorphism. Jehl & Murray (1986) applied this theory to over 150 species of ‘shorebirds’ or ‘waders’ of the suborder Charadrii. We found only four exceptions, two of which have since been found to be unexceptional.

Because female-larger dimorphism is less common in birds, we examined other groups of birds in which females were the larger sex, particularly the raptors, the hawks (Accipitridae), falcons (Falconidae), and owls (Tytonidae and Strigidae), groups that have attracted much attention from ornithologists and generated many *ad hoc* hypotheses (Mueller & Meyer, 1985). We found that in each case, when males were the smaller sex, they engaged in acrobatic aerial display associated with courtship or territoriality (Jehl & Murray, 1986).

(5) Discussion

I contend that this theory is not wrong because it follows the falsificationist philosophy of Popper, because it is put in the form of the deductive-

nomological model of Hempel & Oppenheim (1948), or because I have not explicitly stated all of the assumptions, such as number theory, as required by the semanticists (Thompson, 1989). If it is wrong, it should be shown to be inconsistent with empirical data. This requires showing that at least one of the deduced (or not yet deduced) predictions is contradicted by evidence.

I think that we should understand more about the evolution of clutch size, mating systems, and sexual size dimorphism in birds and other organisms with a single deductive theory than we do with the dozens of *ad hoc* hypotheses that now 'explain' these phenomena (Tables 1–3). Until contradictory evidence is discovered, we must decide whether we are better off with a single theory of three laws explaining the biological facts than with dozens of *ad hoc*, untestable hypotheses that this theory supplants. That is a psychological and social decision (Kuhn, 1970).

X. CONCLUSIONS

I have proposed a syntactic, deductive-nomological theory of evolution by natural selection, which explains the evolution of life-history traits, such as clutch size, age of first breeding, mating system, and sexual size dimorphism of birds and some other animals. Its complete scope remains to be discovered. No one has yet offered a counterargument or an inconsistent fact. One day it may be falsified, but only because one of its deductions is found to be inconsistent with the empirical facts. It is not wrong because it is consistent with Popper's falsificationist philosophy or with Hempel and Oppenheim's deductive-nomological model. It is not wrong because I have not recounted the laws of arithmetic or Mendel's laws or other assumptions of which I am unaware.

This proposal does not end the search for and development of predictive theory in biology. It marks the beginning of a more rigorous formulation and appraisal of biological theories. Instead of proposing *ad hoc* hypotheses, which really are not falsifiable, about the selective advantage of some trait, biologists should be proposing what they imagine to be the initial conditions of the deductive-nomological theory of natural selection, which in combination with the laws explain the evolution of that trait. The test will be to determine whether the proposed initial conditions lead to the evolution of the traits being considered. This is essentially what

biologists are doing now, but inasmuch as they are unfamiliar with the logic of the deductive-nomological model, their thinking is fuzzy and their testing of the theory of natural selection is not rigorous. For example, ornithologists noticed that some populations suffered greater predation on the contents of nests (eggs and nestlings). Skutch (1949) proposed what has become called the nest-predation hypothesis. The proposed selective advantage of the small size of clutches in the tropics was that a smaller brood would have a better chance of surviving because smaller broods would make less noise and require fewer trips by the parents to the nests. The hypothesis is perfectly logical and has been accepted by other ornithologists (Perrins, 1977; Slagsvold, 1982; Martin, 1988, 1992). Equation (2), however, shows us that total predation of nest contents reduces $\sum_i^n P_i$ and partial predation results in a smaller $\sum_x \lambda_x$, both of which indicate that populations suffering greater predation should have larger clutches rather than smaller, contrary to the nest predation hypothesis, but, as noted above, consistent with the few available data (Martin, 1988).

Many of the *ad hoc* hypotheses now proposed to explain this or that biological fact (some listed in Tables 1–3) may actually correspond to the initial conditions of the deductive-nomological theory whose laws are described above. Many biologists have a good understanding of the factors affecting the evolution of the traits they study, but their unfamiliarity with the structure of inductive and deductive theories impedes progress in their developing logically rigorous theory.

With regard to explaining a population's fluctuations and mean size (Section VII.4), there seem to be two laws worth considering as an alternative to the concept of density-dependent regulation (Murray, 1979, 2000c): (i) *a population with constant age-specific rates of survival and constant initial size of cohorts maintains a steady state* (where steady state is understood to refer to a population that is fluctuating within upper and lower boundaries and with a long-term growth rate of zero), and (ii), as first discovered by Lotka (1922), *in the absence of changes in age-specific birth and death rates, a population will eventually establish a stable age distribution*.

West, Brown & Enquist (1997) have proposed what I think may be good candidates for predictive, universal laws in physiology, but the laws, initial conditions, and consequences of their argument are not clearly identified. I have no doubt that there are other universal laws and predictive theories in ecology, evolution, and biology to be discovered. I

do not know what they are, but I do know that only those imaginative investigators who believe they are there to be discovered will discover them.

Nevertheless, inasmuch as almost all of biological theory seems to comprise dozens of *ad hoc* hypotheses (several listed in Tables 1–3), which do little more than describe some correlation between one feature of an organism with some feature of the environment, I think that theoretical (i.e. explanatory) biology is not scientific. In so far as the deductive-nomological theory on the evolution of life-history traits is seemingly, at this time, undiscussible among ecologists and evolutionary biologists because they are unfamiliar with the structure of deductive theory, I again think that theoretical biology cannot be construed to be scientific.

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