



Evolutionary Insights Should Not Be Wasted

Stephen C. Stearns; Paul Schmid-Hempel

Oikos, Vol. 49, No. 1. (May, 1987), pp. 118-125.

Stable URL:

<http://links.jstor.org/sici?sici=0030-1299%28198705%2949%3A1%3C118%3AEISNBW%3E2.0.CO%3B2-E>

Oikos is currently published by Nordic Society Oikos.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/oikos.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Thompson, N. S. 1981. Towards a falsifiable theory of evolution. – In: Bateson, P. P. G. and Klopfer, P. H. (eds), *Perspectives in ethology*. Vol. 4, *Advantages of diversity*. Plenum Press, New York. pp. 51–74.

Williams, G. C. 1966. *Adaptation and natural selection. A cri-*

tique of some current evolutionary thought. – Princeton Univ. Press, Princeton, NJ.

Williams, M. B. 1970. Deducing the consequences of evolution: a mathematical model. – *J. Theor. Biol.* 29: 343–385.

Evolutionary insights should not be wasted

Stephen C. Stearns and Paul Schmid-Hempel, Zoologisches Inst. der Universität, Rheinsprung 9, CH-4051 Basel, Switzerland

Summary. In reply to Pierce and Ollason's critique of optimization techniques in general and foraging theory in particular, we discuss the logic and use of optimality approaches. Most of their argument is based on a misinterpretation of the underlying logic of optimization theory and, more generally, of basic tenets of the scientific method. We agree with some points – not new ones – towards the end of their list – in particular with certain problems encountered when analyzing foraging behaviour.

Introduction

That there are problems with using optimization theory in ecology and evolution is no news to the research community. However, the precise sense in which the technique remains valid has not been appreciated in all quarters, as evidenced by Pierce and Ollason's (1987) attack. They arrange their points in decreasing order of importance, but for the following reasons we find ourselves in agreement with them only as they near the end of their series.

First, in analyzing some problems that arise in modeling behaviour, they have generalized their critique to an attack not just on adaptationist thinking in biology but on the general role of theory in science. Even if the situation in optimal foraging were as bad as they think – and it is not – their statement would still be an unjustified exaggeration. Secondly, their argument is based on a misapprehension of the claims of optimality modelers, whose conception of the organism and of constraints on the evolutionary process is much more sophisticated than Pierce and Ollason are willing to acknowledge. There is not much glory and often much confusion to be gained in the destruction of a straw man.

We have chosen to reply not because these issues are poorly understood by researchers, but because a published attack on optimization, especially one as flawed as this, might confuse to the field by misrepresenting its accomplishments and its current status. We begin our comments at a general level, then finish with a discussion of specific points raised by Pierce and Ollason. It is inevitable that some of our points have already

been discussed in the literature (e.g. Oster and Wilson 1978, Maynard Smith 1978, McNeill Alexander 1982).

1. Defining fitness

Pierce and Ollason make heavy going on several points where closer attention to basic evolutionary theory would eliminate the problems before they arose. First, there is the apparently troublesome term, "fitness". Pierce and Ollason state explicitly, in their Appendix, that if fitness is taken to mean reproductive output, then it has no explanatory content. This is their version of the old accusation that evolutionary theory is circular because it predicts the survival of the fittest, but defines "fittest" as those that reproduce and survive most successfully. On the one hand, such remarks ignore the broad palette of fitness measures that are available for help in making predictions. On the other, such remarks ignore the fundamentally circular nature of deep axioms in all branches of science. We consider the existing diversity of fitness measures first.

In nature, organisms are born, reproduce, and die. We observe the descendants, and in trying to make sense of the patterns that we see, we invent abstract terms, like "natural selection," "fitness," "adaptation," and so forth. These terms help in explaining patterns, making predictions, and constructing consistent interpretations of observations that would otherwise appear to be unrelated. Thus the justification for any definition of the basic terms is practical.

While a term like "fitness" may be used loosely in evolutionary chat, in any specific model, whether in population genetics, optimal foraging, or life-history theory, the term has a concrete and quite unambiguous technical meaning. The meaning may vary from field to field, but in any given context it is clear and, for the purposes of the problem being analyzed, it is rarely if ever a circular definition. In population genetics, the meaning of fitness (usually W), is "that parameter best representing differential reproductive success in such a way that one can predict changes in gene frequencies." Note that fitness serves to help predict changes in gene fre-

quencies, not to predict which individual organisms survive. In life-history evolution, the meaning of fitness (usually r) is "that parameter which incorporates age-specific effects on differential reproductive success and trade-offs in such a way that the optimal integration of the life-history traits can be predicted." Note that fitness in this context is not used to predict who will survive, but how the life history traits should be adjusted to one another to optimize survival and reproduction. It plays the role of an axiom at a deeper level than the ideas under immediate scrutiny.

In most models of foraging behaviour, a short-term measure of reward, such as maximization of the net rate of energy gain, is used. As in life-history theory, a fitness definition is a deeper axiom, and the immediate problem is, given the definition, to predict the optimal adjustment of the foraging parameters. Note that there is no such thing as a well worked-out "optimal foraging theory", as Pierce and Ollason appear to believe, but rather a set of models used to analyze particular situations.

In all three situations, the fitness measures are local tokens for the general notion of fitness. All are short-term measures of relative abundance defined on grounds of practicality (they function in equations that produce interesting solutions) and plausibility (they accord with the most straightforward interpretations of natural selection). Surely there is no fault in being practical, plausible, and straightforward. Moreover, some such measure is unavoidable for the solution of well-posed evolutionary problems.

The notion of life-time reproductive success, shared as a measure of fitness by several fields, has gained popularity because it helps to make successful predictions and logically consistent connections among observations. It therefore enjoys a privileged position as the reference measure of fitness. People working on optimal foraging theory agree that short-term measures of daily or hourly reward must be connected to and in some sense translated into life-time reproductive success to make their work become logically consistent with evolutionary theory, and indeed the issue is being dealt with (e.g. McNamara and Houston 1986). People working in other fields of behavioral ecology, sexual selection, and life-history evolution use this measure because it is straightforward and has not failed them yet. However, the general discussion of fitness measures has already gone well beyond single-generation definitions of reproductive success. The questions of short-term versus long-term measures, and measures of abundance versus measures of risk-minimization, are under investigation in several contexts (Stearns 1986). While results have not come easily, because the problems are technically difficult, the general problem of defining fitness is recognized, it is being worked on, and some progress is being made.

Evidently fitness measures are embedded in a hierarchy of evolutionary problems. Most of us work with

local measures that differ from problem to problem. Only as local problems get solved, and agreement arises on the best measures to use, are the deeper problems of general consistency confronted. As yet, no unified measure of fitness has been discovered that will function well in all the various areas explored by biologists.

2. Is circularity always a bad thing?

We all learn that circular reasoning is to be avoided, but the term "circular" has several meanings. It is of course senseless to recover in the conclusions the assumptions one has made at the outset, especially if the data have had no opportunity to affect the outcome. A good example of this kind of mistake is the assertion that there is an inverse and empirical relationship between population growth rate and generation time. Because that relationship is implicit in the equation used to estimate both variables, no other outcome is possible. This kind of circularity lies at the empirical interface between ideas and observations and should be avoided.

With "deep" axioms used to build large-scale theories – Newtonian dynamics, quantum mechanics, thermodynamics, evolutionary theory – a different, necessary, and advantageous kind of circularity is encountered. In Newtonian mechanics, because $\text{Force} = \text{Mass} \times \text{Acceleration}$, it is circular – or perhaps better, tautological to say that $\text{Acceleration} = \text{Force}/\text{Mass}$. In making that transformation, one is simply asserting that the relationships among basic elements should be preserved under the logical transformations permitted on the system. In evolutionary theory, the deep axiom is that types with superior reproductive performance will be better represented in future generations. Because the statement is tautological, it is useful, for the tautology is a guarantee of logical consistency at the deepest level of the theory. The question here is really about the consistency of theories, where tautology is not only appropriate but precisely what one seeks to demonstrate through carrying out a proof.

The axiom itself is almost never directly under test, but that does not mean that it cannot be tested. It is tested by being incorporated, along with ancillary assumptions specific to each problem, into models that do make testable predictions. If the predictions are falsified, one checks the ancillary assumptions and the logical consistency of the submodels first, before one questions the deep axiom, because the deep axiom has previously proved helpful in the solution of a wide range of problems. This is certainly the case with the fitness axiom in evolutionary theory. Only if the submodels fail in many different areas and if that failure can be traced back to the inappropriateness of the deep axioms does one begin to question them. Until then, changing the deep axioms would cause one to lose more in terms of problems solved in the past than one would gain in problems not yet solved in the present.

The logical structure of evolutionary theory, although

less elaborate, differs in no significant respect from that of physical theory. To accuse evolutionary theory of being empty or circular because its deep axioms are tautological is no criticism at all, for that characterizes all scientific theories.

3. The claims of optimization are limited

The initial application of optimality theory to evolutionary problems produced an over-reaction. Some reacted to the idea the optimality modellers were suggesting that everything about the organism was “perfect”. Others reacted to the notion that evolution could maximize anything at all. The first was based on a misunderstanding of the claims of the theory, and the second, we think, on a misapprehension of the capacity of evolution to refine the design of small pieces of an organism’s morphology, behaviour, and life history.

Optimality modellers in evolutionary ecology have never claimed that all aspects of organisms are optimally adapted to their environments. The idea that they were making this claim is a mistake with two explanations. First, the word “optimal” has one meaning in common usage and quite another in technical usage. In common usage, it simply means “the best possible”. In technical usage, it always means “the best possible under the given boundary conditions”. Secondly, much attention has been paid to optimal predictions, much less to the boundary conditions on which they are based. If one looks carefully at what optimality modellers actually do, one finds that when they enjoy success, they have incorporated lineage-specific biological constraints into their models as appropriate mathematical boundary conditions. This means that they are analyzing local adaptation within a framework of historical constraints, and often the scope for local adaptation is quite limited.

Optimality theory is simply a tool used to make the notion of local adaptation precise. It does rely on the assumption that enough genetic variation is present to permit a thorough local exploration of phenotype space, so that the optimum can be located. This assumption, however, is well justified, for one of the major results in evolutionary biology in the last 20 years is that much more genetic variation is present in natural populations than had been expected. This result holds not just for isozymes, but for metric traits with strong associations with fitness. Nevertheless, the claims of optimality theorists are limited. They recognize the roles of history and constraint and incorporate them in their models as boundary conditions. They could not make their predictions without acknowledging constraints, for their problems would not then be precisely enough posed to force solutions. The portion of organismal adaptation that can be successfully analyzed with optimality techniques is probably small. Therefore when success comes, it should be cherished, for it will probably remain rare when viewed in the context of biology as a whole.

4. The changing-environment argument

Pierce and Ollason argue that because environments constantly change, adaptations to current conditions are impossible, for we can only see the results of past selection. This argument hinges (1) on the relative balance between the rate of evolution and the rate of environmental change and (2) on the definition of what constitutes the selective environment of a trait.

Our estimates of the rate of evolution – and therefore of the likelihood of local adaptation – have been substantially improved. As already stated, there is now evidence for considerable genetic variation in natural populations. Moreover, work over the last half-century has produced examples of quite rapid evolutionary change at a number of levels, e.g. the evolution of disease resistance in Australian rabbits, the evolution of pesticide resistance in flies and mosquitoes, the evolution of drug resistance in bacteria, the evolution of life history traits in salmon and mosquitofish. Thus local adaptation should in principle be possible in many cases through environmental tracking, and in some cases this has actually been demonstrated.

Two other objections to the “pull of the past” argument, both relating to what drives selection, further reduce its force. First, the most important element in the selective environment of any trait is not the external environment itself but the other traits making up that organism. The organism is above all an integrated unit whose parts must function together if the organism is to survive. These relationships among traits within organisms remain relatively constant through time and in fact characterize entire lineages of ancient origin. Thus to the extent that adaptations can be seen as examples of intra-organismal integration, there has been plenty of time for selection to explore phenotype space and locate local adaptive peaks.

Secondly, organisms select the environments in which they live, and to a considerable extent they are able to use this capacity to remain in the same microenvironment despite the major climatic, geological, and biological changes going on around them. Phoronids, for example, are good examples of “living fossils” that have probably inhabited shallow, sandy-bottomed, marine environments for several hundred million years, remaining in the conditions under which they are successful.

It may appear to be contradictory to say, on the one hand, that evolution can be rapid and then, on the other, to say that optimization is possible because evolution is slow. However, that would be a failure to recognize important features of organismal structure. Traits that are invariant within lineages by definition are evolving very slowly. They create a framework of historical constraints. Within this framework, other traits that vary primarily within species evolve more rapidly. It is the latter class of traits in which we can expect to connect adaptations to environmental conditions with

optimality techniques. In fact, as mentioned above, such analysis can only be made if the lineage-specific constraints are incorporated in the optimality analysis as appropriate boundary conditions.

Probably more important than “the pull of the past” is gene flow among habitats with strongly differing selection pressures. It is possible to demonstrate that such gene flow, especially in organisms with moderate to low fecundities, can produce organisms that are maladapted to local circumstances (Stearns and Sage 1980). However, highly fecund organisms overcome this problem with local selection in early stages of the life history, as Turkington’s elegant experiments on adaptations of field herbs to their immediate neighbors have shown (Turkington and Harper 1979, Aarssen and Turkington 1985).

5. Examples of use of and problems with optimization

Arguments about logical foundations are for most scientists not nearly as convincing as demonstrations of empirical success. Krebs et al. (1983; see also Stephens and Krebs, in press) have critically reviewed many examples of the application of optimality techniques to foraging behaviour. They listed several cases where the models used were inappropriate and the conclusions were invalid. This does not detract from the fact that in many of the other cases that they discuss, this approach led to successful predictions about animal behaviour.

There are many fields within evolutionary biology where the optimality approach has successfully been used; we have listed some in Tab. 1. Since discussion of each would make this paper unwieldy, we invite the interested reader to go through them and make up his own mind about the results produced by this approach.

Naturally there are problems with using optimization techniques in evolutionary biology. Although most of them also arise in other scientific methods, the issues are probably clearer with optimality – in itself an advantage.

Usually, tests verify or falsify assumptions by examining predictions. However, one can make correct predictions with incorrect assumptions, which therefore should be verified. This point is often neglected in optimality analyses. Furthermore, alternative hypotheses (models) can yield predictions which are also consistent with the observations. Many studies lack alternative hypotheses, consider only one model, and run the risk of premature claims of success.

An important problem arises when some of the predictions are rejected while others are confirmed. Strictly speaking, the hypothesis should be discarded. However, some failures are inevitable when a simple model is applied to a complex situation. When the failure stems from a specific part of the model, e.g. not perfect choice of the more profitable food but partial preference, it can help to generate better models (Rechten et al. 1983), or lead to reconsideration of the stochastic na-

Tab. 1. Examples of optimization approaches.

Field	Problem	Reference
Foraging	Load size to deliver to central place in bees and starlings Choice of diet	Schmid-Hempel et al. (1985) Kacelnik (1986) Krebs and Avery (1985)
Life-history	Allocation of resources to growth or reproduction	Macevicz and Oster (1976) Stearns and Koella (1986)
Sex allocation	Ratio of male/female offspring under different ecological condition	Hamilton (1967) Charnov (1982)
Biomechanics	Efficient locomotion	McNeill Alexander (1982)
Mating strategy	Duration of copulation	Parker (1978)
Social organisation	Helping behaviour	Reyer (1985)
Dispersion	Placing offspring to different sites	Hamilton and May (1977)
Territories	Holding territories or being a satellite	Davies and Houston (1981)

ture of the process (Stephens 1986). It is “normal” procedure in science not to reject theories simply because they sometimes fail, either because alternatives are not available, or because the theory makes other correct predictions considered valuable. For example, classical mechanics is used for most problems in technology although it makes incorrect predictions in strongly accelerated systems. The same could be argued about models in chemistry that are used to make predictions about chemical bonds, and so on. Pierce and Ollason’s criterion, consistently applied, would lead us to discard some fields of science that are much more successful than optimal foraging.

A problem pertinent to foraging theories is the relation between the quantity maximized by the animal’s behaviour and its fitness. This issue is rarely addressed in foraging studies, but in principle it would be possible to investigate this link empirically, and in some types of optimization theory the connection is direct and evident: foraging for hosts in which to lay eggs by parasitic wasps; allocation into offspring of different sexes; mating duration in dung flies; evolution of developmental rules to determine age and size at maturity.

6. What optimization brings us

Basic contributions. The application of mathematical optimization to problems in evolution and ecology has made several basic contributions. Perhaps the most significant are the clarification of the relationship between

adaptation and constraint and the idea that the most significant factors producing natural selection on a single trait are the other parts of the same organism. In other words, the woolliness of the term “adaptation” has been replaced in certain cases by precision.

Moreover, optimization techniques have been central to the growth of all the specialties making up evolutionary ecology: life-history theory, sex-allocation theory, behavioural ecology and sociobiology. Only if one views the growth of all these fields as having little value would one be inclined to belittle the optimization approach. In approaching that judgement, one should recall two points. In no other area of evolutionary biology have tighter connections between theory and observation been made, and in no other area of evolutionary biology has the rejection or refinement of hypotheses been faster or more efficient. The excitement and dynamism of evolutionary ecology have resulted from the willingness of its practitioners to build simple models that make testable assumptions, then learn from the consequences. Optimality theory and evolutionary thinking have played key roles in making this possible (Stearns 1982).

Quantitative predictions. Optimality models are often able to make quantitative predictions which encounter especially stringent tests. In some cases (e.g. Cowie 1977, Stearns and Crandall 1981, Schmid-Hempel et al. 1985, Stearns and Koella 1986) the predictions are surprisingly accurate, in others (Charnov 1982) they are qualitatively correct but quantitatively less accurate. To anyone who has honestly confronted the complexity of organisms and environments, the ability of simple models to explain a large portion of the variation in any trait, or the qualitative direction of variation in a large number of cases, has to be impressive. Either these models have distilled certain key features of the biology concerned, or they contain a circularity that honest criticism has not yet detected. The stringency of test associated with quantitative predictions jeopardizes Pierce and Ollason's claim that optimality models cannot be tested. Not only can they be tested, they can be tested with unusual rigor.

Evaluation of assumptions. The act of building a model makes clear which assumptions are needed and thus clarifies the problem being analyzed. For example, in considering the foraging cycle of bees (Schmid-Hempel et al. 1985) or starlings (Kacelnik 1984), one must first ask which decisions are taken before the foraging bout begins then which decisions are made on the spot. Bees have to decide on what load to bring back to the nest, but they have already decided to forage at this particular place and time of day. In building a model, one breaks a large problem down into smaller ones that can be individually tested. The approach also identifies those variables for which especially good data are needed to make predictions – the cost of begging in star-

ling chicks, the cost of transporting nectar loads by worker bees, the relationships between size and fecundity and size and offspring mortality in organisms deciding about reproduction, and so forth.

These claims for modelling will appeal to those with a taste for reductionist analysis, but not to those who claim that scientific problems can be solved through a holistic methodology – a methodology we have never seen produce results. Since Pierce and Ollason appear to be among the latter, we do not expect them to be impressed or convinced by these remarks.

Heuristic value. The heuristic value of the optimality approach is vividly demonstrated by the present discussion, which has led several scientists to confront the foundations of their fields. On a deeper level, however, rests a more effective reply to Pierce and Ollason's contention that arguments from heuristic value are not convincing. We claim that there is no other justification for any approach to a scientific problem, that heuristic value is the only criterion we have to judge the relative methods of contending hypotheses and models.

Here we must be careful to define exactly what we mean by heuristic. It is the entire set of features that make it a good idea in practice to use the model to organize research – its simplicity, generality, capacity to synthesize previously unrelated observations into a coherent framework and to make testable predictions, as well as to motivate scientists to clarify their thinking and to gather appropriate data. It is not what remains of a model's worth after it has been demonstrated that the model's assumptions are faulty and its predictions are failures, i.g. the strictly sociological or historical impact on the scientific process of a model that has been seen to be faulty. That is what Pierce and Ollason appear to mean by “heuristic”. All models are eventually shown to be faulty, even the most successful. What matters is the degree of intermediate success and the rate at which the model creates the conditions for its own replacement by something better. In these regards, optimality models are doing pretty well.

7. Specific answers to Pierce and Ollason's criticisms

We wish to answer the specific points raised by the authors, insofar as they have not already been discussed.

What does natural selection maximize? We do not know what or whether natural selection maximizes, but it is plausible to suggest that if natural selection does maximize anything, it is the parts of the organism that are not under evolutionary constraint, and that the maximization has something to do with survival and reproduction, whether in the short or the long term. This general statement of research strategy can be translated through different fitness definitions into specific models that make testable predictions. Pierce and Ollason's misgivings about fitness reveal a lack of understanding on

their part about these issues, as evidenced – among other things – by their statement that “optimal foraging theory predicts that the rate of energy intake will be maximized only if ...”. This is in fact not a prediction, but a plausible assumption made on other grounds; curiously enough, Pierce and Ollason, correctly, reverse this logic under their Point 5.

Animals are not designed. To assert that evolution is a tinkerer does not refute the validity of the analogy with design. The use of the word “design” may mislead the layman, but there is no harm in its use by experts, for vitalism as a scientific proposition has been dead for a long time. Pierce and Ollason’s critique is strongly linked to the argument that what held in the past may not hold in the present. We have already discussed several reasons to think that evolutionary explanations based on present conditions are possible. Pierce and Ollason’s objection that the selective environment is too variable to produce well adapted traits ignores what strikes every observer of nature: that organisms possess beautifully constructed organs and behavioural strategies to survive and reproduce, and that convergent phenomena can be observed in unrelated lineages. More importantly, they also do not recognize that the key factors generating selection on traits are either the other traits making up the organism or environmental conditions that the organism has itself sought out. To the extent that the basic features of organismal design remain stable over long periods of time, the selective environment remains constant and provides ample opportunity for selection to refine designs that may be subject to optimality analysis.

Optimal strategies may not occur in nature. Of course optimal strategies may not occur in nature. Lineage specific constraints with their origin in the fixation of traits quite plausibly prevent optimization in a global context (Stearns 1987). Otherwise, it would be hard to see why organisms come in recognizable packages that we call species. In this sense, the points raised by the authors – which restate arguments raised by Gould and Lewontin (1979) – are certainly valid. However, the problem is not that the optimal variants may not exist, but to identify those parts of organisms in which we can expect to see local adaptation, and those parts that are so historically constrained that it would be more fruitful to view them as boundary conditions than as optimizable traits. Careful comparative analysis shows promise of being able to make this dissection (Stearns 1987).

The existence of optimal strategies is untestable. Pierce and Ollason raise three objections about functional explanations. First, they say, “since it is impossible to know the function of behaviour a priori, if the observed behaviour appears not to be optimal, it may simply be that the function of the behaviour was misidentified”. True enough, but in that case we have learned some-

thing about what the function might not be, and can look further for what it is. Secondly, they say, “Even if the observed behaviour appears to be optimal, it is possible that the behaviour really has a different function, to which it is not optimally adapted”. Because alternative explanations exist for all scientific observations, this statement has no force. That which explains everything explains nothing, and judgements of the relative merits of contending hypotheses are made on other grounds. Thirdly, in saying, “Although most students of foraging behaviour admit that the assumption of optimality cannot be tested, it seems to be forgotten that this means there can be no evidence for optimal foraging”, they appear to forget the structure of scientific ideas. Optimality is a deep axiom used to build particular models with ancillary assumptions. These models can be tested, and if they all failed and proved useless, optimality as a tool would be discarded because it would have been proven useless. Only because such models continue to function in organizing research programs is their common deep assumption retained.

Functional hypotheses are untestable. Pierce and Ollason make two points which – they think – demonstrate that functional hypotheses are untestable. First, they state that because models simplify reality, they distort it, and that assumptions must be tested as well as predictions. Otherwise, the model under test may make the right predictions for the wrong reasons. We agree entirely. Most competent scientists do check assumptions as well as predictions, if not always in the same paper, then in successive publications. However, the fact that assumptions as well as predictions must be checked says nothing about whether functional hypotheses are testable.

Secondly, they assert that one will always be able “to identify a set of environmental characteristics with respect to which observed behaviour is consistent with a particular functional hypothesis, but this process is entirely circular”. It is not. While the environment and the organism may each be complex enough so that many different matchings of behaviour with environment can be generated, it is precisely the function of models to reduce the number of such permitted matchings to a minimum.

Pierce and Ollason finally doubt the value of the “inverse optimality” method (McFarland 1977) where goal functions maximized by the animal’s behaviour are derived from empirical data, rather than the other way round. We agree that this matter has not been settled yet; it is too early to judge the merits of the approach. Yet, viewed this way, optimality could be a useful tool for identifying the constraints on the behaviour under investigation. The approach deserves wider consideration as an interesting and potentially useful provisional hypothesis.

Optimal foraging models have not been tested. That many published tests of optimal foraging are invalid be-

cause some model assumptions have been violated is no news (see Krebs et al. 1983). That assumptions can independently be tested has already been discussed. Pierce and Ollason wilfully ignore those tests that have revealed the explanatory power of optimality models (also cited in Krebs et al. 1983). Considering the complexity of the problems, it is certainly unfair to dismiss the whole approach on the grounds that most models consider only one variable to be under the organism's control. They then deliberately ignore attempts to develop more sophisticated models incorporating two or more variables and the possible trade-offs between them (e.g. Engen and Stenseth 1986, Ydenberg and Houston 1986).

Pierce and Ollason, in the tradition of logical positivism, regret that most studies accept hypotheses rather than rejecting them. It certainly is no shame that some of our ideas seem to be working. While it has long been claimed that one can reject a hypothesis with more certainty than one can confirm it (Popper 1934), this does not mean that a confirmation has no value. For only after a series of confirmations – or failures to reject – do we decide that a hypothesis might have something to it. Moreover, one can reject hypotheses for the wrong reasons (e.g. type I errors in statistics). There is no intrinsic difference between the two procedures. We do agree, however, that usually not enough alternative explanations are tested.

Pierce and Ollason further maintain that with more data, published fits between model predictions and observations would disappear. In some cases, we believe, this would indeed be the case. Collecting a large data base is a virtue often neglected. But this argument does no damage to the approach itself as it is easily tested by collecting more data – which we assume Pierce and Ollason, feeling the force of their own argument, are currently doing.

When models fail in their predictions, researchers often invoke additional assumptions to “rescue” their analysis. Insofar as this procedure contains ad hoc arguments that lack any justification we agree with Pierce and Ollason that it should be avoided and provides no support for the interpretation under consideration. However, every working theorist has seen models fail in specific ways suggestive of forgotten or overlooked constraints. These particular failures provide a basis for further refinement of the models; the procedure is thus not circular, but cyclic and progressive.

Optimal foraging models have not been upheld. We have previously dealt with the arguments that Pierce and Ollason use to make their case and believe they not only have no force, but reveal lack of understanding of how optimization works.

The heuristic value of optimization models and epilogue. The authors' arguments about why these models have no heuristic value are actually not clear to us. In the last

two sections, we see no real arguments, just polemic statements requiring no answer.

8. What directions should the optimization approach take?

For any research program, this is an important question. Since we do not believe that optimization is a waste of time, we would like to mention some directions likely to produce results.

(1) The models should be made more realistic in specific ways. For example, concepts of game theory will increase in importance as the influence of other individuals on the decision-maker is recognized.

(2) Optimality analyses of short-term processes should be linked to differential reproductive success as part of life-history strategies. This problem is of paramount importance.

(3) Most of the concepts used in optimization theory are elegantly simple and of powerful generality – the marginal value theorem in foraging behaviour or the Shaw-Mohler equation for sex allocation. But precisely because they are general, it is often difficult to assert to which particular situation they should apply. Thus, we need to investigate the proximal links connecting general ideas to local conditions.

(4) Knowledge from related fields should be used to identify and check the assumptions of the models. Here the most pressing need is to bring an understanding of the evolution of lineage-specific constraints into evolutionary ecology, and thereby to rationalize within a comparative framework the identification of boundary conditions and places to expect local adaptation.

Acknowledgements – We thank the staff of Villa Cassel, Riederalp, Kanton Wallis, and the Swiss Nature Conservancy for providing an excellent working environment, and the students and staff of the 1986 Feldpraktikum in Populationsbiologie for a stimulating intellectual climate. This work was supported by Swiss National Science Foundation Grants 3.642.0 and 3.272.0.85.

References

- Aarssen, L. W. and Turkington, R. 1985. Biotic specialization between neighboring genotypes in *Lolium perenne* and *Trifolium repens* from a permanent pasture. – J. Ecol. 73: 605–614.
- Charnov, E. R. 1982. The theory of sex allocation. – Princeton Univ. Press, Princeton, NJ.
- Cowie, R. J. 1977. Optimal foraging in great tits, *Parus major*. – Nature, Lond. 268: 137–139.
- Davies, N. B. and Houston, A. I. 1981. Owners and satellites: the economics of territory defense in the pied wagtail, *Motacilla alba*. – J. Anim. Ecol. 56: 621–634.
- Engen, S. and Stenseth, N. C. 1984. A general version of optimal foraging: the effect of simultaneous encounters. – Theor. Pop. Biol. 26: 192–204.
- Gould, S. J. and Lewontin, R. C. 1979. The spandrels of San Marco and the Panglossian Paradigm: a critique of the adaptationist programme. – Proc. Roy. Soc. 205: 581–598.

- Hamilton, W. D. 1967. Extraordinary sex ratios. – *Science* 156: 477–488.
- and May, R. M. 1977. Dispersal in stable habitats. – *Nature*, Lond. 269: 578–581.
- Kacelnik, A. 1986. Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. – *J. Anim. Ecol.* 55: 283–300.
- Krebs, J. R. and Avery, A. I. 1985. Central place foraging in the European bee-eater, *Merops apiaster*. – *J. Anim. Ecol.* 54: 459–472.
- , Stephens, D. W., and Sutherland, W. J. 1983. Perspectives in optimal foraging. – In: Clark, G. A. (ed.), *Perspectives in ornithology*, Cambridge Univ. Press, New York.
- Macevitz, S. and Oster, G. F. 1976. Modeling social insect populations. II: optimal reproductive strategies in annual social insects. – *Behav. Ecol. Sociobiol.* 1: 265–282.
- Maynard Smith, J. 1978. Optimization theory in evolution. – *Ann. Rev. Ecol. Syst.* 9: 31–56.
- McFarland, D. J. 1977. Decision making in animals. – *Nature*, Lond. 269: 15–21.
- McNamara, J. and Houston, A. I. 1986. The common currency for behavioural decisions. – *Am. Nat.* (in press).
- McNeill Alexander, R. 1982. *Optima for animals*. – Edward Arnold, London.
- Oster, G. F. and Wilson, E. O. 1978. *Caste and ecology in the social insects*. – Princeton Univ. Press, Princeton, NJ.
- Parker, G. A. 1978. Searching for mates. – In: Krebs, J. R. and Davies, N. B. (eds.), *Behavioural ecology*. Blackwell, Oxford, pp. 214–244.
- Pierce, G. J. and Ollason, J. G. 1987. Eight reasons why optimal foraging theory is a complete waste of time. – *Oikos* 49: 111–118.
- Popper, K. R. 1934. *Logik der Forschung*. – Wien.
- Rechten, C., Avery, M. I., and Stevens, T. A. 1983. Optimal prey selection: why do Great Tits show partial preferences? – *Anim. Behav.* 31: 576–584.
- Reyer, H.-U. 1985. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Coryle nidis*). – *Anim. Behav.* 32: 1167–1178.
- Schmid-Hempel, P., Kacelnik, A., and Houston, A. I. 1985. Honeybees maximize efficiency by not filling their crop. – *Behav. Ecol. Sociobiol.* 17: 61–66.
- Stearns, S. C. 1982. The emergence of evolution and ecology as experimental sciences. – *Persp. Biol. Med.* 25: 621–648.
- 1986. Natural selection and fitness, adaptation and constraint. – In: Raup, D. and Jablonski, D. (eds.), *Patterns and processes in the history of life*. Dahlem Conference Reports, Springer, Berlin, pp. 23–44.
- 1987. Comparative and experimental approaches to the evolutionary ecology of development. – In Chaline, R. and David, B. (eds.), *Evolution et développement* (in press).
- and Sage, R. D. 1980. Maladaptation in a marginal population of the mosquitofish, *Gambusia affinis*. – *Evolution* 34: 65–75.
- and Crandall, R. E. 1981. Quantitative predictions of delayed maturity. – *Evolution* 35: 455–463.
- and Koella, J. 1986. The evolution of phenotypic plasticity in life history traits: Predictions of norms of reaction for age- and size-at-maturity. – *Evolution* 40: 893–913.
- Stephens, D. W. 1986. How important are partial preferences? – *Anim. Behav.* 33: 667–669.
- and Krebs, J. R. (in press). *Foraging theory*. – Princeton Univ. Press, Princeton, NJ.
- Turkington, R. and Harper, J. L. 1979. The growth, distribution and neighbor relationships of *Trifolium repens* in a permanent pasture. IV. Fine-scale biotic differentiation. – *J. Ecol.* 67: 245–254.
- Ydenberg, R. C. and Houston, A. I. 1986. Optimal trade-offs between competing behavioral demands in the Great Tit. – *Anim. Behav.* 34: 1041–1050.