ELSEVIER

Behavioural Processes 46 (1999) 189–199

BEHAVIOURAL PROCESSES

www.elsevier.com/locate/behavproc

The proximate and the ultimate: past, present, and future

Donald A. Dewsbury *

Department of Psychology, University of Florida, Gainesville, FL 32611-2250, USA

Received 27 October 1998; received in revised form 22 March 1999; accepted 22 March 1999

Abstract

The distinctions inherent in the proximate–ultimate dichotomy have a long history. I examined several issues related to this distinction. It is important that distinctions among different problem areas be made so that the type of answer presented in research in animal behavior is appropriate for the type of questions being asked. This may require more than the two-way distinction between the proximate and the ultimate. I suggest that such terms as ‘function’, ‘ultimate’, and ‘ultimate causation’ be re-evaluated. Methodological problems encountered when measuring differential adaptive consequences of alternative behavioral patterns and when using proximate stimulus control to infer adaptive significance require further consideration.

Keywords: Proximate; Ultimate; Function; Evolution; Development; Control

1. Introduction

All psychologists and other life scientists tread in the footsteps of Aristotle. Following his predecessors, it was he who proposed the first systematic taxonomy of different types of causation. These are generally taught using a statue as a pedagogic device. Aristotle's *material cause* is the stuff of which the statue is composed, perhaps marble; the *formal cause* is the shape into which the material has been molded, perhaps the Venus de Milo; the *efficient cause* is the agent of the change, the sculptor. Especially interesting is the fourth variety, the *final cause*, or the purpose of the object. The statue is created to provide a beautiful object that brings pleasure. Why did Aristotle make these distinctions? It was because he believed that various of his predecessors had emphasized one kind of cause at the expense of the others. The early Milesian philosophers focused on material causes; Empedocles stressed efficient causes; Plato focused on formal causes. Aristotle sought a more comprehensive view incorporating all four aspects (Taylor, 1967).

The concept of causation has been a topic of dispute among philosophers ever since. With the development of modern science, the four Aristotelian causes were relegated to courses in the history of philosophy. Nevertheless it is interesting that Aristotle was trying to do exactly what later biologists, such as Ernst Mayr and Niko Tinbergen, later attempted—to make a distinction among different questions and to find a balance in their consideration.

* Tel.: +1-352-3920601; fax: +1-352-3927985.

E-mail address: dewsbury@psych.ufl.edu (D.A. Dewsbury)

PII: S0376-6357(99)00035-2

Most problematical of the Aristotelian causes for modern scientists is the concept of final cause. They see no indwelling purpose in the universe in general or in life in particular, although the behavior of individuals may be goal-directed in a certain limited sense. Yet the human mind naturally seems to seek comfort and closure with the idea that the world is purposive. In some respects the concept of the ultimate replaces that of final cause and provides the closure sought. The modern biologist's *adaptive significance* has replaced the philosopher's *teleology*; it is fundamentally different and should not be confused with it—but it serves a similar function in our view of nature.

The topic of the proximate and the ultimate can be viewed as a development of Aristotle's four causes and has become focal in the field of Animal Behavior Studies. I shall consider several aspects of the topic: the early history and development of the concept and related concepts, recent views, and, finally, some methodological concerns.

2. The development of the concepts

It is commonplace in the history of science that credit properly goes not to the first individual to express an idea but rather to the individual who develops it and forces it into our consciousness and vocabulary. So it is with the issue at hand.

2.1. The proximate–ultimate distinction

In essence, the proximate–ultimate distinction is that between the causes of behavior that occur within an animal's lifetime and those that precede its life, i.e. evolutionary factors. The underlying ideas inherent in the proximate–ultimate distinction are not new; indeed, the underlying ideas are pervasive. Psychologists need go no further than William James' *1890 Principles of Psychology* to find their expression. James clearly distinguished between the function and the immediate causation of such behavioral patterns as a hen incubating her eggs or a man sitting near a warm stove on a cold day. James did not have the formal concept of the ultimate but understood adaptive preferences as inherent in the nature of the organism as the result of Kantian *a priori* syntheses. But the principle is the same; he wrote:

> Not one man in a billion, when taking his dinner, ever thinks of utility. He eats because the food tastes good and makes him want more. If you ask him *why* he should want to eat more of what tastes like that, instead of revering you as a philosopher he will probably laugh at you for a fool... to the animal which obeys it, every impulse and every step of every instinct shines with its own sufficient light, and seems at the moment the only eternally right and proper thing to do. It is done for its own sake exclusively. What voluptuous thrill may not shake a fly, when she at last discovers the one particular leaf, or carrion, or bit of dung that out of all the world can stimulate her ovipositor to its discharge? Does not the discharge then seem to her the only fitting thing? And need she care or know anything about the future maggot and its food? (James, 1890, vol. II, pp. 386–387)

The proximate–ultimate distinction is inherent in Craig (1918) 'Appetites and Aversions as Constituents of Instincts'. The point is that appetitive behavior, though adaptive, is directed not toward some biological end but rather toward the appearance of an appeted proximate stimulus, which terminates the behavior. Even the mechanist–reflexologist–physiologist Ivan Pavlov wrote of the distinction:

> Under natural conditions the normal animal must respond not only to stimuli which themselves bring benefit or harm, but also to other physical or chemical agencies—waves of sound, light, and the like—which in themselves only *signal* the approach of these stimuli; though it is not the sight and the sound of the beast of prey which is in itself harmful to the smaller animal but its teeth and claws (Pavlov, 1927, 1927p. 14).

Several authors have traced the development of the concept in the 20th century biology (Mayr, 1974; Hailman, 1982; Dewsbury, 1992). The earliest uses were by Huxley (1916) and Baker (1938). Lack (1954) followed Baker and gave prominence to the distinction in the introduction to *The Natural Regulation of Population Numbers*. Mayr (1961) developed the distinction and presented it clearly in a manner that helped to popularize the distinction. Beatty (1994) has shown how Mayr did not come upon the idea suddenly; it grew gradually through the different stages of his career and was already apparent in his writings of 1930. Mayr used the distinction in part in turf wars in defending evolutionary biology first from the mechanical physiologists and later from the molecular biologists. Mayr has returned to the theme of the proximate–ultimate distinction on various occasions and is its outstanding proponent (e.g. Mayr, 1974, 1993).

2.2. Tinbergen's four problems

An overlapping tradition led to a similar distinction that was stated most clearly by Tinbergen (1963). Tinbergen's 'four problems' included those of causation, ontogeny, survival value, and evolution. Tinbergen argued that a complete understanding of a behavioral pattern entails information in all four of these problem areas. The names of the four problems have changed with various authors (see Dewsbury, 1992); I will use immediate causation, development, adaptive significance, and evolutionary history as the labels.

This formulation too had its antecedents. Both Huxley (1942) and Orians (1962) differentiated among causation, adaptive significance, and evolutionary history. Kortlandt (1940a,b) differentiated among five aspects or issues of ethology, form (in space and time), function, ontogeny, and phylogeny (Kortlandt, 1998). Mayr (1961) actually included four forms of causation, ecological, genetic, intrinsic physiological, and extrinsic physiological, in his considerations. Thus, as with Mayr's development of the proximate–ultimate differentiation, Tinbergen is associated with the four-problems concept because of the ways in which he developed and promoted the ideas rather than because he was the first to make these distinctions.

2.3. Merging the proximate–ultimate and the four problems

Contrary to the assertions of some authors, Tinbergen (1963) presented his four problems ungrouped. It was probably Klopfer and Hailman (1972a,b) and Alcock (1975) who were most responsible for merging the concepts of the proximate and the ultimate with Tinbergen's four problems. The result was the familiar formulation that proximate, or how, problems include development and immediate causation and ultimate, or why, questions include adaptive significance and evolutionary history.

3. Recent developments

3.1. Reformulating the system

In recent years various authors have proposed modifications to the structure and function of these distinctions (see Dewsbury, 1992). Several authors (e.g. Sherman, 1988) treated the various problems as a hierarchy, implying that one is of a higher order than another. Other authors prefer to treat the four problems as complementary with each of value in the context of its own domain (e.g. Armstrong, 1991; Dewsbury, 1992).

Dewsbury (1992) pointed out that the four problems share a number of similarities and differences. For example, whereas the problems of evolutionary history and adaptive significance have in common a concern with events that transcend the lives of individuals, it is evolutionary history and development that share the characteristic of demanding historical analysis relative to the behavior at hand. He proposed that it is a mistake to group the questions only according to one property while ignoring the others. He then proposed a new organizational schema that included the genesis (evolution, cultural inheritance, and development), control (external and internal), and consequences (for the individual, environment, and differential reproduction) of behavior. This proposal was criticized by Alcock and Sherman (1994) and defended by Dewsbury (1994). Although I still like the formulation, it has not been widely adopted. In a parallel and independent development, however, Hogan (1994) felt that he surprised his readers in that he considered 'phylogenetic changes to be a causal problem' (p. 6). This is very much in the spirit of my proposed reorganization.

3.2. Changing emphases

For many years, although different scientists tended to emphasize the study of one or more of the four problems, there was easy communication among them. For example, on the program of the Animal Behavior Society (ABS) or in the pages of prominent journals in the field one would find studies of all varieties of problems. In recent years, somewhat paradoxically, however, there has been both a separation and a coming together. Research on the development and immediate causation of behavior has continued to thrive but those studying these problems have become dissociated from their colleagues emphasizing the study of adaptive significance (e.g. Barlow, 1989; Dawkins, 1989; Kennedy, 1992). Studies of evolutionary history have been somewhat rare. *Animal Behaviour*, *Behavioral Ecology*, *Behavioral Ecology* and *Sociobiology*, and other leading journals and organizations, such as the Animal Behavior Society, and the International Society for Behavioral Ecology, have become the province of the study of adaptive significance. Ask someone at an ABS meeting today why an animal performed a certain behavioral pattern and you are virtually assured of getting your questions answered in relation to adaptive significance—one of Tinbergen's four questions. Ask the same question at a meeting of the Society for Neuroscience and you will get a very different answer.

Many authors erroneously write of the differentiation between comparative psychology and ethology as if it were a difference in the problems studied, with ethologists interested in the ultimate and psychologists in the proximate. There are many ways in which to refute this. For one, they should return to the classic textbook that helped to establish the field of animal behavior in biology, Marler and Hamilton (1964) *Mechanisms of Animal Behavior*. The title is appropriate. Throughout the volume the focus is on problems of development and immediate causation. These authors would write a very different book today; whereas the 1966 book dealt primarily with proximate problems, they surely would emphasize ultimate problems in today's climate.

Bradbury and Vehrencamp (1998) have recently provided a masterful summary of a vast amount of literature concerning animal communication. Included is an impressive and comprehensive treatment of proximate aspects of animal communication. However, the conceptual underpinnings of the work are clearly structured around problems of adaptive significance. The sophisticated consideration of proximate factors is structured as constraints on, and mechanisms of, patterns of adaptive significance. I suggest that the reason for these major differences between these two books lies in their dates of publication. The 30-odd years separating them have seen a major shift in the focus of the field.

Drickamer (1998b) plots the changing content of articles in *Animal Behaviour*, supporting this trend. However, Drickamer may underestimate the effect. He points out that for some scientists, probably mainly ecologists, studies of behavior are treated as 'mechanisms'. To one studying behavior and reared on Tinbergen's four questions, this seems perverse. Behavior is that which is to be explained, not a 'mechanism' for anything. If we exclude such studies from the category of mechanisms and include only studies of development and immediate causation, the shift described by Drickamer becomes even more pronounced.

Although students of proximate and ultimate questions have become estranged during this period, a centrifugal trend, in recent years there has also been a centripetal trend—a tendency for individual investigators to consider multiple questions. Dewsbury (1990) summarized the content in a contributed volume on contemporary comparative psychology noting that in many chapters the research programs transcend individual problems and are concerned with more than one problem. There seems to be a developing blending of approaches.

A variation on this theme has appeared in the symposium edited by Drickamer (1998b) and the volume of Real (1994). In this tradition there is again an integration of the study of immediate causation and adaptive significance but the latter is primary with the former subordinate. Thus, the emphasis is upon *mechanisms of* adaptive behavior, that is on the adaptive behavior with studies of mechanism used to reveal the ways in which adaptation is effected. There is much less interest in what an understanding of adaptive significance can contribute to the study of mechanisms. For example, in their discussion of the methods that might be used in integrating the proximate and the ultimate, Drickamer and Gillie (1998) clearly emphasize methods of revealing how proximate mechanisms serve adaptive significance, rather than the converse.

4. Concerns about the future

Having discussed where considerations of this issue have been and appear to be, it is appropriate to consider where it should go. My concerns relate to the language used, the apparent replacement of the four problems with the proximate–ultimate distinction, and methods used in studies of adaptive significance.

4.1. The mischief of words

The first concern is the words that are used in this domain. There are several that appear to be problematical.

4.1.1. Function

Few words have more meanings than does ‘function’. It is commonplace in the literature in Animal Behavior Studies for the term to be used as equivalent to ‘adaptive significance’. Such authors as Burghardt (1973) and Lehner (1979) are quite explicit in this usage. ‘Function’ has long been recognized as a word burdened with a confusing array of alternative meanings for different scientists (e.g. Ruckmich, 1913). In common parlance, the term often refers to the manner in which a mechanism operates, as when an automobile *functions* properly. In biology, when Mayr (1961) promoted the proximate/ultimate distinction, he did so by contrasting the approach in evolutionary biology with that in *functional* biology. The term has numerous meanings. Because of this ambiguity I would like to see the term no longer used to refer to adaptive significance. If it must be used, it should be only together with the word ‘adaptive’, as in ‘adaptive function’.

4.1.2. Ultimate causation

It has become commonplace to refer to proximate versus ultimate *causation* (e.g. Mayr, 1993; Alcock, 1993; Drickamer, 1998a). ‘A cause has traditionally been thought of as that which produces something and in terms of that which is produced, its effect can be explained’ (Taylor, 1967). Obviously, the cause must precede the effect.

I know of no biologists who would argue that an effect can precede its cause. However, they talk and write as if it could. ‘Ultimate causation’ is generally treated as including both evolutionary history and adaptive significance. Clearly, the former is an historical phenomenon that precedes the behavior in question. The adaptive significance, however, is more problematical. To the extent that it is made clear that matters of adaptive significance concern the ways in which the behavior has been beneficial to the animal’s forbears there is no problem. Where current utility is of concern, however, there is a major problem in that the implication is that an event precedes its cause. Alcock (1993), for example, presents a table in which ‘ultimate causes’ are presented as including ‘past and *current* utility of the behavior in reproductive terms’ (p. 4, italics added). It is difficult to see current utility as a cause without drifting into teleology. Again, causes must precede events. As Hogan (1994) put it, ‘the outcome of behavior can never determine its occurrence’ (p. 9). With respect to the issue at hand, I have only minor problems with uses such as ‘ultimate questions’, ‘ultimate considerations’, or ‘ultimate problems’; however, when linked to the word ‘causation’. I believe that a problem occurs.

4.1.3. Ultimate

I do, however, see another problem with the term 'ultimate'. This concerns its surplus meaning. 'Ultimate' can mean, among other things, either the greatest or highest, or the most fundamental. To use 'ultimate' in this way is to imply that ultimate questions are more important than proximate questions. Although surely many evolutionary biologists believe this, it is a form of disciplinary chauvinism not shared by all, such as those funding biological research. 'Ultimate' can also mean distal. 'Distal' is a more acceptable term (see Francis, 1990; Armstrong, 1991). The simplest solution is that of Mayr (1993), who noted that 'I have used in most of my recent papers the term 'evolutionary' instead of ultimate causation' (p. 94). If the distinction is to remain, it would seem best to contrast proximate with evolutionary problems or questions.

To be clear, the issue is not the value of such distinctions but how we talk about them. The words confuse students and often some very distinguished scientists (e.g. Kennedy, 1992). If 'ultimate' is to mean 'evolutionary', why not say what is meant and use the latter term?

4.2. Are two categories enough?

In the 1970s and 1980s Tinbergen's four problems were in vogue. There seems to be a trend in more recent literature to refer to the proximate–ultimate dichotomy at the expense of the four-problem approach (e.g. Drickamer, 1998a,b). Is this for the good? I suggest that it is not.

With respect to proximate problems, although there is admittedly some gray area between problems of development and immediate causation, the distinction is a useful one in differentiating alternative approaches.

I am more concerned, however, with evolutionary problems. The questions asked and methods used in dealing with problems of evolutionary history and adaptive significance can be quite different (see Antonovics, 1987). As noted above, some of the terms that fit problems of evolutionary history are more questionable when applied to adaptive significance. There would seem to be value in the clarity that follows when the distinction is made clear.

An interesting subsidiary problem concerns so-called cultural evolution. Because cultural evolution transcends the lives of individuals it can be classed together with evolutionary changes (e.g. Alcock and Sherman, 1994). Because such changes are non-genetic, however, in the systems usually adopted I would retain it as an ambiguous, intermediate category. The proximate–ultimate distinction does not appear sufficient to encompass all of the distinctions appropriate in the field of Animal Behavior Studies.

5. Methodology

5.1. Methods in the study of adaptive significance

Too little attention has been directed at the systematization of the methods that can be used to make inferences about the adaptive significance of a behavioral pattern (see Dewsbury, 1978). I list some:

5.1.1. Armchair speculation

Surely the least satisfactory is *post-hoc* speculation. One can construct 'just-so stories' that appear reasonable but lack empirical verification.

5.1.2. The experimental method

One systematically manipulates an independent variable, in this case behavior, and examines the effect on a measure likely to affect lifetime reproductive success. The study by De Ruiter (1956) on countershading provides an example.

5.1.3. The method of within-species correlation

This is the same as the experimental method except that, rather than manipulate an independent variable, one takes advantage of naturally occurring variation in nature and correlates it with some measure related to reproductive success. Patterson (1965) study of synchronization of breeding in black-headed gulls provides an example.

5.1.4. Method of adaptive correlation

With this method one examines a variety of species and tries to correlate behavior patterns with ecological conditions to infer selective pressures related to the adaptive significance of the pattern. Cullen (1957) the study of kittiwakes is the type case.

5.1.5. Diallel cross

Although it has gone out of fashion, some suggestive evidence of adaptive significance can be gained from behavior-genetic analysis using the diallel cross method (Bruell, 1964). Dewsbury (1975) this study of copulatory behavior in rats provides an example.

5.1.6. Inferring adaptive significance from proximate control

In this method one determines the proximate conditions under which a behavioral pattern occurs and uses them to infer adaptive significance. For example, Caro (1986) and Alcock (1993) conclude that stotting in Thompson's gazelles is not an alarm signal because the gazelles display the pattern when alone. Further, they reject the anti-ambush hypothesis, that stotting helps the gazelle see possible predators, because stotting occurs in short grass as well as long. Note that one is here considering not the effects of the behavioral pattern but the stimulus control thereof.

In another case Alcock (1993) argues that rape in humans is not related to the subjugation of women because, he argues, if it were, the most effective stimuli for rape would be women in positions of power. The hypothesis that rape is an adaptive strategy is favored because the targets of the rape are typically women in their peak reproductive years.

In recent years the methodology has become increasingly sophisticated as new techniques from molecular biology and mathematical modeling have become prevalent; the underlying logic, however, is basically the same.

5.2. Failure to differentiate among methods

These methods are not always differentiated clearly. For example, in Chapter 1 of his textbook on animal behavior Alcock (1993) uses the example of infanticide in langurs to illustrate the methods used in testing hypotheses about adaptive significance. He first considers consequences using the method of within-species correlation, asking whether the result of infanticide is that infanticidal males reproduce sooner than non-infanticidal males. He then shifts gears, rather subtly, and without differentiating the fundamental difference in method when considering alternative hypotheses. Alcock suggests, in effect, that one way to test among alternative hypotheses is to consider the nature of the proximate stimuli for infanticide, such as whether males kill other males' infants. In yet another application of this method, he asks whether the dead infant provides a sufficient proximate stimulus for eating (i.e. does the langur consume the dead infant). He then asks whether the sufficient proximate conditions for infanticide include human interference. Finally, he asks whether removing a dominant male, thus creating a takeover without male–male aggression, leads to infanticide. In the latter operations, discussed in a section on methodology, the proximate control, rather than the consequences, of the behavior is used to infer adaptive significance without noting the shift of method.

What are needed are (a) a more fully developed taxonomy of methods, (b) study of the conditions under which each is useful, and (c) clear presentations of the assumptions and pitfalls encountered when employing them.

5.3. Problems with measuring consequences

Both the method of within-species correlation and the experimental method rely on the assessment of the effects of variation in the behavior on current reproductive success. This carries with it the assumption that the selective forces operating now are the same as or similar to those operating when the behavioral pattern evolved. Surely this is a parsimonious assumption (Alcock and Sherman, 1994). Nature, however, is not always noted for its parsimony. As the field of evolutionary psychology has developed in recent years there has developed within it a skepticism concerning studies in which alternative behavioral patterns produce different adaptive outcomes (e.g. Tooby and Cosmides, 1992; Crawford, 1993). These authors argue that the mechanisms underlying human behavior may have evolved in the Pleistocene and that they may be expressed in contemporary culture in ways that differ from those at the time when the mechanisms evolved. They argue that we should be very skeptical of studies in which alternative hypotheses are evaluated with respect to current adaptive outcomes and focus instead on the underlying mechanisms. Thus, rather than asking 'how is Susan increasing her fitness by salting her eggs?', we should ask 'What is the nature of the evolved human salt preference mechanisms—if any—that are generating the observed behavior and how did the structure of these mechanisms mesh with the physiological requirements for salt and the opportunities to procure salt in the Pleistocene?' (Tooby and Cosmides, 1992, 1992 p. 55).

Although one assumes that human behavior evolved according the same fundamental principles as that of any other species, it is likely that the current human environment differs from that in the Pleistocene to a greater degree than is true for other species and thus this problem is especially important for human behavior. However, some concern about the applicability of this principle to the behavioral patterns of other species appears warranted.

5.4. Problems with inferring adaptive significance from proximate control

Here I return to a theme I stated earlier (Dewsbury, 1994) with little apparent effect on the field. I believe there is a serious problem with the procedure of inferring adaptive significance from proximate control. The nub of the problem is what has been termed 'rules of thumb' (Krebs and McCleery, 1984). Rules of thumb refer to the proximate behavioral programs that animals appear to follow and which lead them to behave in ways that often approximate optimization. A foraging animal may allocate time among patches not on the basis of its ability to understand the marginal value theorem but, rather, according to a 'giving-up time' rule of thumb that leads it to change patches after a certain period of time without encountering prey. Proximately, a bird may fly south in the fall not because it anticipates cold weather but because of decreasing day length. Females may prefer brightly colored males without understanding the detrimental effects of mating with parasite-laden males and that color may be, in part, a function of parasite load (Hamilton and Zuk, 1982). Proximally, rodents of various species avoid mating with their siblings not by determining kinship directly but, rather, by avoiding mating with partners that are familiar. The fact that there may be no overt struggle between a mother and her young in determining the time of weaning need not imply that there have been no conflicts operating in the evolution of the time of weaning. The whole point of rules of thumb is that there need not be a tight fit between the proximate rule and the adaptive significance.

Earlier (Dewsbury, 1994) I expressed some concern that the proximate rule of thumb can be used as a 'fudge factor' to argue in favor of a model whose fit to data is imperfect. I think this view is correct. However, I also believe the rule of thumb to be a very valuable notion and one that we need to both take seriously and use with caution. I am especially concerned that rules of thumb tend to be invoked when data do not closely match the predictions of a model and are rarely considered when the fit is good.

Often, attempts to infer adaptive significance from proximate control are fraught with hidden assumptions. In the examples mentioned above, it is assumed that the stotting gazelle has fine-tuned its behavior so that it is displayed only under the primary conditions responsible for its evolution. Is it not possible that the gazelle might evolve a rule that says 'stott when you see a predator' with the primary selective force related to intraspecific communication but with no proximate clause directing the animal to withhold the behavior in the absence of conspecifics? Indeed, might that not be safer than delaying so as to pick and choose the conditions under which the pattern is displayed? Similarly, if stotting is related to predator detection, might not the rule direct the animal to stott regardless of the length of grass rather than to measure the grass before making a decision? Do we really believe that the power hypothesis of rape requires that men be more likely to rape more powerful women? I believe that we must treat all attempts to infer adaptive significance from proximate stimulus control with considerable skepticism.

Inherent in this discussion is the realization that evolutionary fine-tuning the stimulus control over a behavioral pattern has costs as well as benefits and when the former outweigh the latter the proximate mechanism may diverge from the underlying selective pressures to an increased extent. In the same spirit Dawkins and Guilford (1991) propose that conventional, and perhaps dishonest, signals may evolve where the costs of assessment to the receiver are so great that they outweigh the benefits of discriminating honest from dishonest signalers.

The practice of using information about proximate stimulus control to infer adaptive significance is widespread. For example, in a recent study the authors predicted that male eastern bluebirds and tree swallows would lower their parental investments if their female partners were removed for two mornings during the period of egg laying (Kempenaers et al., 1998), and in another it was predicted that male chiffchaffs ought to defend larger territories during periods of female fertility than at other times (Rodrigues, 1998). Neither prediction was especially successful. I suggest that it is possible that the fault may lie in the logic of the procedures rather than in the validity of the underlying hypotheses supposedly under test.

Models can be quite elaborate. Curio et al. (1984), for example, developed an elaborate model to predict when great tits should defend their broods depending on such variables as the time of the breeding season, the age of the young, and the number of young in their second broods. The model was successful in predicting effects of several variables. Where it failed, the authors cited ‘proximate factors coupled to the precise breeding area’ (p. 101).

I fully realize that this method is quite widespread in the field of animal behavior studies today. However, I do think that some concern is appropriate.

6. Conclusions

In the field of Animal Behavior Studies, research can be directed at a variety of different questions. It is extremely important that these be differentiated so that there is an appropriate correlation between the kind of question asked and the kind of answer proffered. The ideas underlying the proximate–ultimate distinction and that distinction itself have been in the literature for some time. In recent years the field of animal behavior studies has come to be dominated by questions of adaptive significance.

I have several suggestions:

1. Because of its multiple meanings we should not use the term ‘function’ when we mean ‘adaptive significance’.
2. Although most animal behaviorists have a clear conception of the issues discussed herein, their language sometimes causes confusion for those outside the field. If the proximate–ultimate distinction must be retained, I suggestion that Mayr’s replacement of ‘ultimate’ with ‘evolutionary’ be adopted. Alternatively, ‘distal’ might be acceptable.
3. I suggest that ‘causation’, as used in ‘ultimate causation’, be replaced with terms such as ‘questions’, ‘considerations’, or ‘problems’.
4. The proximate–ultimate distinction is a useful one as far as it goes. However, in collapsing across several different categories of problems some important distinctions are missed. Therefore, a systems such as that proposed by Tinbergen (1963) or Dewsbury (1992) is to be preferred. To be clear, I believe the concepts underlying the proximate–ultimate distinction are quite important; my concern is that they do not go far enough.
5. We need to be careful in inferring adaptive significance in the evolution of behavioral patterns from demonstrations of differential consequences under present-day conditions.
6. We need to be very careful about using proximate information concerning the stimulus conditions under which a behavioral pattern occurs to infer adaptive significance. The proximate mechanism, as with rules of thumb, may be quite different from the selective pressures

responsible for the evolution of the behavioral pattern under consideration.

I remain a pluralist, believing that different scientists should be free to investigate, with appropriate methodology, any of the various problem areas discussed above. There need be no compulsion to address more than one of these areas. However, I believe that there is much to be gained for some of us by doing so. It remains to be seen whether, as suggested by Curio et al. (1984) those studying those studying mechanisms have more to gain from considering issues of adaptive significance than vice versa.

I continue to envisage a balanced field of Animal Behavior Studies such as that envisaged by Tinbergen in which studies of development, immediate causation, evolutionary history, and adaptive significance all flourish, each with equal dignity.

References

Alcock, J., 1975. Animal Behavior: An Evolutionary Approach, 1st ed. Sinauer, Sunderland, MA.

Alcock, J., 1993. Animal Behavior: An Evolutionary Approach. 5th ed. Sinauer, Sunderland, MA.

Alcock, J., Sherman, P., 1994. The utility of the proximate–ultimate dichotomy in ethology. Ethology 96, 58–62.

Antonovics, J., 1987. The evolutionary dys-synthesis: which bottles for which wine? Am. Nat. 129, 321–331.

Armstrong, D.P., 1991. Levels of cause as organizing principles for research in animal behavior. Can. J. Zool. 69, 823–829.

Baker, J.R., 1938. The evolution of breeding seasons. In: G.R. de Beer (Ed.), Essays on Aspects of Functional Biology, Clarendon, Oxford, pp. 161–177.

Barlow, G.W., 1989. Has sociobiology killed ethology or revitalized it? In: Bateson P.P.G., Klopfer P.H. (Eds.), Perspectives in Ethology, vol. 8. Whither Ethology, Plenum, New York, pp. 1–45.

Beatty, J., 1994. The proximate/ultimate distinction in the multiple careers of Ernst Mayr. Biol. Phil. 9, 333–356.

Bradbury, J.W., Vehrencamp, S.L., 1998. Principles of Animal Communication, Sinauer, Sunderland, MA.

Bruell, J., 1964. Inheritance of behavioral and physiological characters of mice and the problem of heterosis. Am. Zool. 4, 125–138.

Burghardt, G.W., 1973. Instinct and innate behavior: Toward an ethological psychology. In: Nevin, J.A. (Ed.), The Study of Behavior, Scott Foresman, Glenview, IL. pp. 321–400.

Caro, T.M., 1986. The functions of stotting in Thomson's gazelles: some tests of the predictions. Anim. Behav. 34, 649–652.

Craig, W., 1918. Appetites and aversions as constituents of instincts. Biol. Bull. 34, 91–107.

Crawford, C.B., 1993. The future of sociobiology: counting babies or studying proximate mechanisms? Trends Ecol. Evol. 8, 183–186.

Cullen, E., 1957. Adaptations in the kittiwake to cliff-nesting. Ibis 99, 275–302.

Curio, E., Regelmann, Zimmermann, U., 1984. The defense of first and second broods by great tit (*Parus major*) parents: A test of predictive sociobiology, Z. Tierpsychol., 66, 101–127.

Dawkins, M.S., 1989. The future of ethology: How many legs are we standing on?. In: Bateson, P.P.G., Klopfer, P.H. (Eds.), Perspectives in Ethology vol. 8. Whither Ethology, Plenum, New York, pp. 47–54.

Dawkins, M.S., Guilford, T., 1991. The corruption of honest signaling. Anim. Behav. 41, 865–873.

De Ruiter, L., 1956. Countershading in caterpillars. Arch. Neer. Zool. 11, 285–341.

Dewsbury, D.A., 1975. A diallel cross study of genetic determinants of copulatory behavior in rats. J. Comp. Physiol. Psychol. 88, 713–722.

Dewsbury, D.A., 1978. Comparative Animal Behavior. McGraw-Hill, New York.

Dewsbury, D.A., 1990. Comparative psychology: Retrospect and prospect. In: Dewsbury D.A. (Ed.), Contemporary Issues in Comparative Psychology, Sinauer, Sunderland, MA, pp. 431–451.

Dewsbury, D.A., 1992. On the problems studied in ethology, comparative psychology, and animal behavior. Ethology 92, 89–107.

Dewsbury, D.A., 1994. On the utility of the proximate–ultimate distinction in the study of animal behavior. Ethology 96, 63–68.

Drickamer, L.C., (Ed.) 1998a. Animal behavior: integration of proximate and ultimate causation, Am. Zool. 38, 39–259.

Drickamer, L.C., 1998b. Vertebrate behavior: integration of proximate and ultimate causation. Am. Zool. 38, 39–42.

Drickamer, L.C., Gillie, L.L., 1998. Integrating proximate and ultimate causation in the study of vertebrate behavior: methods considerations. Am. Zool. 38, 43–58.

Francis, R.C., 1990. Causes, proximate and ultimate. Biol. Phil. 5, 401–415.

Hailman, J.P., 1982. Ontogeny: Toward a general theoretical framework for ethology. In: Bateson, P.P.G., Klopfer, P.H. (Eds.). Perspectives in Ethology, vol. 5, Plenum, New York, 133–189.

Hamilton, W.D., Zuk, M., 1982. Heritable true fitness and bright birds—A role for parasites? Science 218, 384–387.

Hogan, J.A., 1994. The concept of cause in the study of behavior. In: Hogan J.A., Bolhuis J.J. (Eds.), Causal mechanisms of behavioural development, Cambridge University Press, Cambridge, pp. 3–15.

Huxley, J., 1916. Bird-watching and biological science. Auk, 142–161 33, 256–270.

Huxley, J., 1942. Evolution: The Modern Synthesis, Harper, New York.

James, W., 1890. Principles of Psychology (vol. 2), Holt, New York.

Kempenaers, B., Lanctot, R.B., Robertson, R.J., 1998. Certainty of paternity and paternal investment in Eastern bluebirds and tree swallows. Anim. Behav. 55, 845–860.

Kennedy, J.S., 1992. The New Anthropomorphism, Cambridge University Press, Cambridge.

Klopfer, P.H., Hailman, J.P. (Eds.), 1972a. Function and Evolution of Behavior An Historical Sample from the Pens of Ethologists, Reading, MA, Addison-Wesley.

Klopfer, P.H., Hailman, J.P. (Eds.), 1972b. Control and Development of Behavior An Historical Sample from the Pens of Ethologists, Addison-Wesley, Reading, MA.

Kortlandt, A., 1940a. Methode van Onderzoeken en Interpreteren van Doelstrevende Gedragscoördinatie bij het in het Wild Levende Aalscholvers, een in Kolinies Broedende Vogelsoort. Arch. Neerl. Zool. 4, 401–442.

Kortlandt, A., 1940b. Wehselwirkiung Zwischen Instinkten. Arch. Neerl. Zool. 4, 443–520.

Kortlandt, A., 1998, February 14. [Letter to D.A. Dewsbury].

Krebs, J.R., McCleery, R.H., 1984. Optimization and behavioral ecology. In: Krebs J.R., N.B. Davies (Eds.). Behavioural Ecology: An Evolutionary Approach, Sinauer, Sunderland, MA, pp. 91–121.

Lack, D., 1954. The Natural Regulation of Population Numbers, Clarendon, Oxford.

Lehner, P.N., 1979. Handbook of Ethological Methods, Garland, New York.

Marler, P., W.J. Hamilton, III, 1964. Mechanisms of Animal Behavior, Wiley, New York.

Mayr, E., 1961. Cause and effect in biology. Science 134, 1501–1506.

Mayr, E., 1974. Teleological and teleonomic, a new analysis. Boston Stud. Phil. Sci. 14, 91–117.

Mayr, E., 1993. Proximate and ultimate causations. Biol. Phil. 8, 93–94.

Orians, G.H., 1962. Natural selection and ecological theory. Am. Nat. 96, 257–263.

Patterson, I.J., 1965. Timing and spacing of broods in the black-headed gull *Larus ridibundus*. Ibis 107, 433–459.

Pavlov, I.P., 1927. Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex (tr. G.V. Anrep). Oxford University Press, Oxford.

Real, L.A. (Ed.), 1994. Behavioral Mechanisms in Evolutionary Ecology, University of Chicago Press, Chicago.

Rodrigues, M., 1998. No relationship between territory size and the risk of cuckoldry in birds. Anim. Behav. 55, 915–923.

Ruckmich, C.A., 1913. The use of the term *function* in English textbooks of psychology. Am. J. Psychol. 24, 99–123.

Sherman, P.W., 1988. The levels of analysis. Anim. Behav. 36, 616–619.

Taylor, R., 1967. Causation, In: Edwards, P. (Ed.), The Encyclopedia of Philosophy, Macmillan, New York, pp. 56–66.

Tinbergen, N., 1963. On aims and methods of ethology. Z. Tierpsychol. 20, 410–433.

Tooby, J., Cosmides, L., 1992. The Psychological foundations of culture. In: Barkow, J.H., Cosmides, L., Tooby, J. (Eds.), The Adapted Mind Evolutionary Psychology and the Generation of Culture. Oxford, New York, pp. 19–136.