ARTICLE

The Predictive Power of Evolutionary Biology and the Discovery of Eusociality in the Naked Mole-Rat

Stanton Braude

Anti-evolutionists have asserted that evolutionary biology lacks predictive power (Gish 1979; Johnson 1991; Morris 1974, 1989). They still cite Karl Popper's early suggestion that evolutionary theory is untestable because it cannot be used to make predictions, despite the fact that this view has been rejected by philosophers of science and that Popper himself unequivocally reversed this opinion (1978:344-5). Such assertions that evolutionary theory is unpredictive ignore the power of the comparative method in testing both alternative hypotheses and models of evolutionary processes as well as the pervasive implicit tests of evolutionary theory in every aspect of modern biological science. In this paper I will discuss briefly how biologists across disciplines use evolutionary theory as a foundation for understanding biological systems. Next I will give a few examples of how evolutionary biologists test hypotheses about specific modes of selection and evolution. Finally I will discuss, in detail, an example of the extremely successful predictive power of one evolutionary hypothesis.

Pervasive Use of Evolutionary Hypotheses in Biology

"Nothing in biology makes sense except in the light of evolution" (Dobzhansky 1973). Accordingly, biochemists, geneticists, ecologists and medical researchers do not choose their hypotheses randomly. A hypothesis must first be logically consistent to be worth testing. An underlying part of the logic in most biological hypotheses is that the system under study is adaptive, selectively neutral or even maladaptive (but maladaptive in ways that we can understand based on conflicting biological demands or novel circumstances). Maladaptive characters are studied in the context of their unusual nature and the surprise they pose in light of an apparently well adapted biological world. When molecular biologists investigate complex biochemical pathways, gene regulators, or carrier proteins, they are working under the paradigms that the molecules in question serve an adaptive function. Biochemists do not test hypotheses about the beauty of a molecule but about its function (Stryer 1995).

The fact that not all biological systems are adaptive can be confusing, and this confusion has misled some scientists to conclude that evolution is, therefore, irrelevant to understanding particular maladaptive systems. However, evolutionary theory is not limited to explaining adaptations. For example, simple adaptive hypotheses cannot explain senescence, but the study of age-related changes in the potential for future reproduction (reproductive value) and of (pleiotropic) genes that produce a number of different traits has given us the clearest understanding of why senescence has evolved differently in different organisms (Alexander 1987; Charlesworth and Hughes 1996; Williams 1957). Cancer is also best understood as the result of selection working at the cellular level and in conflict with competing selective forces at the individual level (Tomlinson and others 1996).

Biologists across disciplines also indirectly test phylogenetic hypotheses and assumptions when choosing test organisms. When medical researchers want to test the effects of a new drug or treatment, they recognize that the phylogenetic relationship between the model experimental organism and humans is relevant to interpreting results and judging either the efficacy or danger to humans. Results based on rodent studies are given less weight than primate studies because of our more distant common ancestry and the greater divergence that has resulted.

Direct Tests in Evolutionary Biology

Direct tests and predictions about the mode of evolution are conducted daily by evolutionary biologists and population geneticists. However, an arbitrary distinction between micro- and macro-evolutionary processes has been used to devalue tests of evolutionary hypotheses in selection experiments or in insect population cages (where insects can hatch, breed and die for hundreds of generations in the course of an experiment). Population geneticists make predictions and test hypotheses about

Stan Braude has been studying naked mole-rats in the laboratory and field for the past 15 years. He is currently on the faculty of the International Center for Tropical Ecology at the University of Missouri-St. Louis and at Washington University in St. Louis.

the mode of evolution. In population cages, petri dishes or growth media, population geneticists test hypotheses about evolutionary change in controlled populations (for example Carson and others 1994; Goodnight and Stevens 1997; Templeton 1996). In wild populations, population geneticists look at gene frequencies within species or populations in order to test hypotheses about relatively recent evolutionary events (for example Crandall and Templeton 1993; Routman and Templeton 1994; Templeton and others 1993).

Ecologists and conservation biologists use evolutionary theory to interpret the relationships we see in wild communities and to predict how those communities will be affected by changes and environmental pressures (for example Georgiatis and others 1994; Losos and others 1997; Templeton and Read 1994). While much of current ecological theory is complex and multivariate, MacArthur and Wilson (1967) were able to make rather simple and testable predictions about the diversity of species on islands of different sizes and distances from a mainland. In addition, behavioral ecologists make predictive hypotheses about the trends we expect to see across a wide variety of taxa (Alexander and others 1979; Harvey and Pagel 1991; Martins 1996; Ryan 1990).

In the examples cited above, predictions from and tests of evolutionary theory fit into two general categories: how evolution works in specific cases and circumstances, and what evolution has produced in response to particular circumstances. Ecologists, phylogeneticists, and population geneticists are interested in the subtle details of how evolution works. In testing adaptive hypotheses about how their particular biological system works, other biologists are testing predictions of what evolution has produced. The underlying paradigm is that evolution has generally produced adaptive systems and structures.

The uses of evolutionary theory to make these various predictive hypotheses have also been criticized as being *post hoc* since we already know what has evolved but cannot do simple experiments and predict what will evolve. This line of reasoning not only ignores all the population cage experiments in evolutionary biology but, if true, would lead to the classification of astronomy as unscientific as well, since we cannot manipulate the cosmos. The multitude of minute, precise predictions about the locations of known planets and stars in tomorrow night's sky are analogous to the specific predictions that are made in comparative tests by evolutionary biologists.

Occasionally, however, more striking predictions are made. In 1845 John Couch Adams and Urbain Jean Joseph Leverrier both predicted the presence of an unseen planet which affects the orbit of Uranus. It was not until the following year that Neptune was discovered as they had predicted.

Richard D Alexander has made a similarly striking prediction based on first principles of the evolution of social behavior. Although common in social insects, eusociality—the social system with a queen and sterile workers—was unknown in any other taxa. Under the appropriate set of conditions, Alexander predicted, evolution ought to produce a eusocial vertebrate, even though eusociality in the naked mole-rat (or any other vertebrate) was unknown at the time.

A Fertile Use of Inductive and Deductive Logic

The roots of Alexander's prediction go back to questions raised by Darwin over 100 years prior. In his chapter titled "Difficulties with the theory" Darwin addressed the problem that sterile workers in social insect colonies pose for natural selection. How could natural selection cause differences between queen bees and workers if the workers are sterile? Darwin guessed that in these cases selection is acting between families or hives.

In 1964 William Hamilton formalized this idea of kin selection and suggested that eusocial colonies with queens and workers have evolved many times in the ants, bees, and wasps because of their unusual genetic system. In these hymenopteran insects, males have one set of chromosomes (haploid) and females have two sets (diploid); this is called haplodiploidy. As a consequence of this genetic peculiarity, sister workers in these insects are more closely related to each other than they would be to their own offspring. Consequently, they contribute to the propagation of a greater proportion of their genes by helping to rear siblings than by producing offspring themselves.

How could natural selection cause differences between queen bees and workers if the workers are sterile?

In 1974 entomologist and evolutionary theorist Richard Alexander argued that "subsocial" behavior (that is parental care) and the opportunity for parental manipulation were even more powerful factors in the evolution of social behavior in insects (Alexander 1974). Across taxa, parental behavior correlates much more strongly with eusociality than does haplodiploidy (Andersson 1984; Alexander and others 1991). Alexander's critics argued that if parental care is a crucial precursor to eusociality, we should expect eusociality to have also evolved among the highly parental vertebrates: birds and mammals. Alexander could have pointed out that there are far fewer species of birds and mammals than there are species of insects, or that birds and mammals have only existed for 160 million and 250 million years respectively (Eisenberg 1981; Wetly 1979) while insects have existed for 350 million years (Borror and others 1989). Instead he asked himself what characteristics a eusocial vertebrate would have if it had evolved.

Alexander based his answer on his understanding of the selective forces involved in the evolution of insect eusociality and hypothesized a eusocial vertebrate. He created a 12-part model for a eusocial vertebrate, based on this body of theory. He had no idea that a mammal with these characteristics existed.

Alexander predicted that a eusocial vertebrate's nest should be (1) safe, (2) expandable, and (3) in or near an abundance of food that can (4) be obtained with little risk. These characteristics follow from the general characteristics of primitive termite nests inside logs. The nest must be safe or it will be exploited as a rich food source for predators. It must be expandable so that workers can enhance the value of the nest. It must be supplied with safe abundant food so that large groups can live together with little competition over food or over who must retrieve it.

The limitations of the nest characteristics suggested that the animal would be (5) completely subterranean because few logs or trees are large enough to house large colonies of vertebrates. Being subterranean further suggested that the eusocial vertebrate would be (6) a mammal and even more specifically (7) a rodent since many rodents nest underground. The primary food of the hypothetical vertebrate would be (8) large underground roots and tubers because the small grassy roots and grubs that moles feed on are so scattered that they are better exploited by lone individuals and would inhibit rather than encourage the evolution of eusociality.

...mammalogist Terry Vaughan suggested to Alexander that his hypothetical eusocial rodent was a "perfect description" of the naked mole-rat...

The major predator of the hypothetical vertebrate would have to be (9) able to enter the burrow but be deterred by the heroic acts of one or a few individuals. This would allow for the evolution of divergent life lengths and reproductive value curves between workers and reproductives. Predators fitting this description would include snakes.

The eusocial vertebrate was also expected to (10) live in the wet-dry tropics because plants there are more likely to produce large roots and tubers that store water and nutrients to help them survive the dry periods. The soil would need to be (11) hard clay because otherwise the nest would not be safe from digging predators. These two characteristics further suggested (12) the open woodland or scrub of Africa.

Alexander described this social vertebrate in a series of guest lectures at North Carolina State University, University of Kansas, University of Texas, Colorado State University, Arizona State University, University of Arizona, and Northern Arizona University at Flagstaff in 1975 and 1976. At Flagstaff, mammalogist Terry Vaughan suggested to Alexander that his hypothetical eusocial rodent was a "perfect description" of the naked mole-rat *Heterocephalus glaber*. He further described the burrowing East African mammal and suggested that Alexander contact Jennifer Jarvis, an authority on African mole-rats. Jarvis had studied the ecology and physiology of naked mole-rats but at that time nothing was known about their social system. Subsequent field and laboratory observations have confirmed that they are in fact eusocial, as Alexander's model had predicted, and that the other elements of his model are accurate as well (Braude and Lacey 1992; Jarvis 1981; Sherman and others 1991; Sherman and others 1992). This case demonstrates one type of predictive power in modern evolutionary theory.

Evolutionary biologists are making new discoveries every day. To suggest that evolutionary biology is either untestable or unpredictive ignores their vast body of work including the dramatic discovery of eusociality in the naked mole-rat based on clear understanding of the selective forces leading to the evolution of social behavior.

Acknowledgments: Many thanks to Nancy Berg, Keith Butler and two anonymous reviewers for their valuable comments and suggestions.

References

Alexander RD. The evolution of social behavior. *Annual Review of Ecology and Systematics* 1974; 5:326-83.

Alexander RD, Hoogland JL, Howard RD, Noonan KM, Sherman PW. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. In: Chagnon N and Irons W eds. *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. North Scituate (MA): Duxbury Press, 1979. p 402-35.

Alexander RD. *The Biology of Moral Systems*. Hawthorn (NY): Aldine de Gruyter, 1987.

Alexander RD, Crespi B, Noonan K. The evolution of eusociality. In: Sherman P, Jarvis J, Alexander RD, eds. *The Biology of the Naked Mole-Rat*. Princeton: Princeton University Press, 1991. p 3-44.

Andersson M. The evolution of eusociality. *Annual Review of Ecology and Systematics* 1984; 15:165-89.

Borror D, Triplehorn C, Johnson N. *The Study of Insects*. 6th ed. Philadelphia: Saunders College Publishing, 1989.

Braude S, Lacey E. The underground society. *The Sciences* 1992; 32:23-8.

Carson HL, Val FC, Templeton AR. Change in male secondary sexual characters in artificial interspecific hybrid populations. *Proceedings of the National Academy of Sciences of the United States of America* 1994; 91(14):6315-8.

Charlesworth B, Hughes KA. Age-specific inbreeding depression and components of genetic sequence variance in relation to the evolution of senescence. *Proceedings of the National Academy of Sciences of the United States of America* 1996; 93(12):6140-5.

Crandall K, Templeton AR. Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. *Genetics* 1993; 134(3): 959-69.

Darwin CR. *On the Origin of Species*. New York: Collier Books, 1859.

Dobzhansky T. Nothing in biology makes sense except in the light of evolution. *American Biology Teacher*. 1973; 35:125-9.

Eisenberg J. *The Mammalian Radiations*. Chicago: University of Chicago Press, 1981.

Georgiatis N, Bischof L, Templeton A, Patton J, Karesh W, Western D. Structure and history of African elephant populations: I. Eastern and southern Africa. *Journal of Heredity* 1994; 85(2): 100-4.

Gish DT. *Evolution? The Fossils Say No!* San Diego: Creation-Life Publishers, 1979.

Goodnight CJ, Stevens L. Experimental studies of group selection: What do they tell us about group selection in nature? *American Naturalist* 1997; 150(Supplement):59-79.

Harvey P, Pagel M. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press, 1991.

Jarvis JUM. Eusociality in a mammal: Cooperative breeding in naked mole rat colonies. *Science* 1981; 212:571-3.

Johnson PK. *Darwin on Trial*. Washington: Regnery Gateway, 1991.

Losos JB, Warheit KI, Schoener TW. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 1997; 387:70-3.

MacArthur RH, Wilson EO. *The Theory of Island Biogeography*. Princeton: Princeton University Press, 1967.

Martins E. *Phylogenies and the Comparative Method in Animal Behavior*. Oxford: Oxford University Press, 1996.

Morris HM. *Scientific Creationism*. San Diego: Creation-Life Publishers, 1974.

Morris HM. *The Long War Against God*. Grand Rapids (MI): Baker Book House, 1989.

Popper KR. *Objective Knowledge: An Evolutionary Approach*. Oxford: Oxford University Press, 1972.

Popper KR. Natural selection and the emergence of mind. *Dialectica* 1978; 32:339-55.

Routman E, Templeton AR. Parsimony, molecular evolution and biogeography: The case of the North American giant salamander. *Evolution* 1994; 48(6):1799-809.

Ryan MJ. Sensory systems, sexual selection, and sensory exploitation. *Oxford Surveys in Evolutionary Biology* 1990; 7:157-95.

Sherman PW, Jarvis JUM, Alexander RD. *The Biology of the Naked Mole-Rat*. Princeton: Princeton University Press, 1991.

Sherman PW, Jarvis JUM, Braude S. Naked mole-rats. *Scientific American* 1992; 267(2):72-8.

Stryer L. *Biochemistry* 4th Ed. New York: Freeman, 1995.

Templeton AR. Experimental evidence for the Genetic-transilience model of speciation. *Evolution* 1996; 50(2): 909-15.

Templeton AR, Read B. Inbreeding: One word, several meanings, much confusion. In Loeschke V, Tomuik J, Jain SK eds. *Conservation Genetics*. Basel: Birkhauser Verlag, 1994.

Templeton AR, Hollocher H, Johnston IS. The molecular through ecological genetics of abnormal abdomen in *Drosophila mercatorum*. Female phenotypic expression on natural genetic backgrounds and in natural environments. *Genetics* 1993; 134(2): 475-85.

Tomlinson IPM, Movelli MR, Bodmer WF. The mutation rate and cancer. *Proceedings of the National Academy of Sciences of the United States of America* 1996; 93(25):14800-3.

Welty J. *The Life of Birds*. 2nd ed. Philadelphia: Saunders College Publishing, 1979.

Williams G. Pleiotropy, natural selection and the evolution of senescence. *Evolution* 1957; 11:398-411.

AUTHOR'S ADDRESS:

Stan Braude
Biology Department
Campus Box 1137
Washington University
One Brookings Drive
St. Louis MO 63130
email: braude@wustlb.wustl.edu

THE GALAPAGOS TOUR IS OPEN DUE TO CANCELLATIONS, SEE PAGE 31 FOR DETAILS

REPORTS OF THE NATIONAL CENTER FOR SCIENCE EDUCATION

Volume 17, Number 4

JULY/AUG, 1997

CONTINUES *NCSE REPORTS* & *CREATION/EVOLUTION*

Lamarck vs. Darwin: Dueling Theories

Discovery of Eusociality in the Naked Mole-Rat

The ICR and the "Bible Code"

Creationists React to "Jurassic Park" Sequel