
Foundations of *Classic Papers*

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Evolution of Behavior

Approaches to Studying
Behavioral Change*Stevan J. Arnold and H. Jane Brockmann*

Introduction

Understanding the evolution of behavior requires both a description of how behavior has changed over time and an analysis of why behavior has changed. Accordingly, we have grouped into two sections a selection of classic papers on the evolution of behavior. Papers in the first section document the phylogenetic history of behavior, and those in the second section provide analyses of the selective pressures that can produce new adaptations in behavior. Within this second section, we sorted papers into four approaches: comparative, correlational, experimental, and modeling. This categorization is not exhaustive. We have, for example, not included any studies that impose selection in experimental populations and docu-

ment evolutionary response. Likewise, the section on behavioral adaptation neglects papers that focus on inheritance, constraints, drift, and a host of other important topics.

In each section we have summarized primary research questions and considered the classic papers in the context of past and present conceptual developments. Our aim is not to produce a definitive history of science, but rather to guide the reader to related papers and developments. Early papers can be found in Burghardt (1985), and the early history of the field also is discussed by Klopfer and Hailman (1967). Richards (1987) discussed perspectives on behavioral evolution in the nineteenth century.

Phylogenetic History of Behavior

Studies of behavioral phylogeny ask two questions: (1) How do displays and other behavior patterns originate? and (2) What are the steps by which behavior and its underlying mechanisms evolve? Attention to these questions has a long history, beginning with Darwin (1859, 1871, 1872). Comparative studies addressing both issues blossomed during the period from 1940 to 1965 (e.g., Crane 1949; Daanje 1950; Baerends and Baerends-van Roon 1950; Tinbergen 1952; Jacobs 1953; Morris 1956, 1958; Moynihan 1962; Crook 1964; and van Tets 1965). For an overview of work during this period, see Hinde (1966). From about 1965 and until recently, comparative work languished, perhaps because the attention of ethologists was shifted by sociobiology and behavioral ecology. In recent years, however, comparative ethology has begun to flower again. The basic issues of historical transformation of behavior are the same, but methods are more explicit and rigorous (Brooks and McLennan 1991; Harvey and Pagel 1991). The new methods in comparative work are based on two principles. First, reconstruction of history requires a model of evolutionary process (Felsenstein 1973, 1985). In the past, such models were implicit and their connections to the inference of history were unstated. The contemporary challenge is to make explicit the models or assumptions about process that lurk behind studies of history. Second, the inference of phylogeny is a statistical undertaking (Felsenstein 1983, 1988). Although each group of species has only one actual phylogeny, that actual phylogeny is estimated by a set of more or less plausible alternative phylogenies. Statistical methods can be used to evaluate those alternatives. From this brief overview of past work and ongoing developments, we

now turn to the articles about behavioral phylogeny that are reproduced in this volume.

We chose papers by Konrad Lorenz (1941) and Howard Evans (1962) from a large field of candidate papers published during the heyday of ethology. These two papers are outstanding exemplars for two reasons. First, a large number of taxa are surveyed in each study. The size of each survey allows us to view many examples of behavioral differentiation. Second, results are displayed on a phylogeny. Such graphical portrayals are increasingly common and are likely to be the norm in the future (e.g., McLennan et al. 1988; Lauder 1990; Carpenter 1989; Proctor 1991; Langtimm and Dewsbury 1991). The reader may be surprised by the scant attention to methodology in these early papers by Lorenz and Evans. Until the advent of numerical taxonomy (Sokal and Sneath 1963) and its descendants (e.g., Farris 1988; Felsenstein 1991; Swofford 1991), it was normal practice to present phylogenetic conclusions with virtually no discussion of how those conclusions were reached. Phylogenetic conclusions were simply meant to represent the opinion of the author. That opinion was often offered without any justification of methods. The notion that methods of arriving at phylogenetic conclusions could be codified and compared did not appear until later.

Lorenz (1941, 1971) provides an important early illustration of the phylogenetic study of behavior. In addition to the fascinating discussion of display origins and modifications, this paper often is remembered for its "shaving brush" portrayal of a phylogeny (Lorenz 1971, p. 114), which enables the reader to see the evolution of behavioral traits on the tree. Limitations of space did not allow

us to reproduce the entire paper. Instead, we have included sections from the beginning and end of the paper that discuss aims and methodology. To give the flavor of the ethograms and discussions that constitute the bulk of the paper, we have excerpted a section describing displays performed by the mallard drake and their possible origins. The interested reader may wish to compare Lorenz's phylogeny with those of Sibley and Ahlquist (1990) and Livezey (1991), and Lorenz's discussion of display evolution with McKinney's (1975).

Like Lorenz, Evans (1962) surveys a behaviorally diverse array of species and dissects the history of behavioral modification. Their approaches, however, are fundamentally different. Lorenz uses behavior to deduce phylogenetic relationships of his species and interprets the history of behavioral change in light of those relationships. Evans, in contrast, uses a phylogeny based on a separate (independent) set of characters, focusing on larval morphology (Evans 1959). He puts his behavioral traits on that phylogeny (fig. 6) and then discusses evolutionary

trends in the behavior. This contrast in the methods used by Lorenz and Evans is mirrored by an ongoing debate in systematic biology. Proponents of the "total evidence" school argue that all available characters should be included in the construction of a phylogeny (Eernisse and Kluge 1993). Alternatively, one can argue that one set of characters should be used to construct the trees, so that the history of a second set of independent characters can be reconstructed on the tree, as in Evans (1962). By following this procedure, inferences about the evolution of the second set of characters are not confounded with the process of constructing the tree (Felsenstein 1988). Evans (1962) also uses the illustrative technique of having the phylogenetic tree grow up through a series of behavioral layers. The underlying concept was introduced by Simpson (1953), who referred to the layers as "adaptive zones." Phylogenetic studies of behavior recently have taken on new life and often are imbedded within the comparative approach, which we consider next.

Four Approaches to the Study of Adaptation

Four approaches have been used to study behavioral adaptation: comparative, correlational, experimental and modeling. One approach is not superior to the others. Rather, each asks different questions and should be viewed as complementary to the others (Endler 1986; Arnold 1988). In the future, the most illuminating studies of behavioral adaptation are likely to use two or more of these approaches in combination.

Comparative Approach

The comparative approach to adaptation attempts to identify the selective pres-

ures responsible for evolutionary change in behavior or other traits. In modern practice, one begins with a phylogeny of taxa based on traits other than, and presumably independent of, those under scrutiny (e.g., molecular or morphological data) or with a phylogeny based on a combined behavior-nonbehavior data set (Grimaldi 1987; Sillen-Tullberg 1988; Arntzen and Sparreboom 1989; Ember-ton 1994; Titus and Larson 1995). Behavioral traits are placed on this phylogeny to reconstruct the probable history of behavioral change (procedures reviewed by Maddison and Maddison 1992). Next, aspects of the ecological or social envi-

ronment that represent putative selective pressures are placed on the tree and their history is reconstructed. Finally, the statistical association between changes in behavior and changes in selective pressures is assessed (Coddington 1988; Harvey and Pagel 1991). The complete version of the comparative approach to adaptation goes beyond the phylogenetic studies of Lorenz (1941) and Evans (1962) by placing both behaviors and putative selection pressures on the tree and analyzing their statistical association. The approach is correlational (as is the method described next), but the time scale is commonly on the order of thousands or even millions of generations. Several early ethological papers use the spirit of the comparative approach to studying adaptation. Cullen's (1957) reprinted here, is a particularly fine example.

Cullen's (1957) comparison of a cliff-nesting gull, the kittiwake (*Rissa tridactyla*), with its ground-nesting relatives is a classic because of its success in identifying selective pressures. Cullen begins by arguing that the recent ancestor of the kittiwake and its congener, *Rissa brevirostris*, was a ground-nesting species. She reaches this conclusion because the most closely related genus to *Rissa* is the genus *Larus*, and nearly all of the many species in that genus nest on the ground. This form of argument is known today as an outgroup comparison (Brooks and McLennan 1991). (A modern practitioner also would ask whether the sister group to *Rissa* and *Larus* is a ground- or a cliff-nester.) Cullen then describes a large number of behavioral and morphological differences between the kittiwake and ground-nesting gulls. Most important, she relates nearly all of these differences to: (1) relaxation of selection due to the absence of predation, and (2) the special selective pressures that derive from cliff-nesting. Cullen's paper stands out be-

cause of the large number of traits that come under scrutiny and because of the plausibility of her selection arguments. Perhaps many niche shifts precipitate large suites of new adaptations. Cullen encourages us to look closely for interlocking sets of adaptations. Her predictions later were tested by others who worked on other cliff-nesting species. Indeed, other cliff-nesters like Galapagos Swallow-tailed gulls (Hailman 1965) or Noddy Terns (Cullen and Ashmole 1963) should show similar adaptations.

Correlational Approach

The correlational approach asks whether natural variation in behavior is statistically associated with differences in fitness within a population. In the most informative version of the approach, the behavioral traits of individuals are scored and then those individuals are followed through time so that their survivorship and/or reproduction can be assessed. In contrast to the comparative approach, the time scale for assessing selection with the correlational approach is typically a single generation or less and the focus is on a single population. Selection is measured in statistical terms that can be related to the selection coefficients that are used in equations for evolutionary change (Lande and Arnold 1983; Phillips and Arnold 1989). The correlational approach, with its emphasis on individual reproductive success, has its roots with Pearson at University College and Weldon at Cambridge (Provine 1971); in addition to the research groups of Lack and Tinbergen at Oxford. The recent surge of correlational studies of behavior has been reviewed by Fedigan (1983), Wiley (1991), Ryan and Keddy-Hector (1992), and Searcy (1992). A notable early paper using the correlational approach to behavior was Patterson (1965), who showed

that gulls nesting on the periphery of a colony are less successful than those nesting in the middle, and that gulls nesting in synchrony were more successful than those that were asynchronous. Although this approach is useful for identifying possible selective pressures, one can not be sure of cause and effect. Gulls nesting in the middle of the colony may be more successful because they are older or in better condition, and not because they derive any protection from their colonial nesting behavior. For lack of space we have not reproduced any papers using the correlational approach.

Experimental Approach

The experimental approach to the study of adaptation asks whether a particular behavior or other trait is capable of affecting reproductive success. Usually the reproductive success of the two treatment groups is compared. In one group the expression of behavior is exaggerated, reduced or altogether eliminated. In the other group (the control), a sham operation of exaggeration, reduction or elimination is performed, but behavioral expression is unaltered and coincides with the average behavioral state in the population. The design and statistical analysis of such experiments is discussed in many textbooks (e.g., Cox 1958; Martin and Bateson 1968).

Behavioral experiments are particularly informative when they are performed in the field, for then they can tell us whether the normal array of predators and other selective agents are capable of exerting selection under natural circumstances. Successful field experiments are much admired because they are often difficult to do. The trick is to manipulate behavior while leaving everything else unchanged, have the selective agents do their work, and be able to score the re-

sults. This choreography is more difficult than it sounds! Selective agents such as free-ranging crows are especially prone to be uncooperative. Niko Tinbergen was one of the first masters of this approach.

In Tinbergen et al. (1962), the authors ask whether predators are the likely selective agents maintaining egg-shell removal behavior in a gull population. We have included only the parts of the paper that focus on the consequences of egg-shell removal. Due to space limitations we have not reproduced the middle section of the paper on the stimulus control of egg-shell recognition by parent gulls. It is worth noting, however, that this study, in its entirety, provides an excellent example of the value of studying both proximate and ultimate factors. The authors motivate their study in their opening paragraph by noting that egg-shell removal: (1) shows interesting evolutionary diversification (in particular, kittiwakes do not show egg-shell removal), and (2) is likely to be advantageous in some way because it is performed at apparent cost to the hatching nestling. The account of the experiments used to tackle the issue of survival value is illuminating because it takes us through the process of refining hypotheses. The authors systematically vary one characteristic at a time and maintain large sample sizes in each experiment. Finally, the discussion is worthy of special attention as the authors place egg-shell removal in the context of other traits that protect the nest from predators.

Models of Selection and Evolution

Models of selection and evolution ask whether it is logically feasible for a particular selective process to exert selection and cause evolutionary change. Models cannot tell us whether selection and evolution actually will occur in the natural

world, but they can tell us whether our logic is sound or flawed. Models also can help us organize concepts so that our empirical work is focused on the right issues.

Hamilton's (1964) papers provided a new perspective on the evolution of social behavior. From the standpoint of style, the papers are unusual because they combine a novel theoretical viewpoint, the classical mechanics of population genetics, and a rich field of biological examples and applications. We have reproduced only the first of the pair of papers because of space constraint. The second, longer paper deals with applications of the model. The first paper is difficult to read, even for those trained in theoretical population genetics, but it develops the important concept of inclusive fitness and explains its utility in understanding the evolution of social behavior. It may help the reader to realize that the description of the model is directed at two issues. The first part (pp. 2-7) develops an equation for the change in frequency of a gene that affects social behavior; inclusive fitness plays a key role in this equation (eq. 2 on p. 6). The second part (pp. 7-8) is concerned with how inclusive fitness itself will change over time. In genetical models that do not involve social interactions, average fitness tends to show an increase over evolutionary time; Hamilton wants to know if inclusive fitness shows a similar property. Despite misleading claims in many articles and textbooks, average fitness (whether personal or inclusive) is not always maximized by evolution (Wright 1969; Lewontin 1978). The paper ends with a discussion of an inequality (p. 16) that has come to be known as Hamilton's Rule. In the second paper, Hamilton gives Haldane (1955) credit for expressing the crux of the idea: "Let us suppose that you carry a rare gene which affects your be-

havior so that you jump into a flooded river and save a child, but you have one chance in ten of being drowned. . . . If the child is your own child or your brother or sister, there is an even chance that the child will also have this gene, so five such genes will be saved in children for one lost in an adult. If you save a grandchild or a nephew the advantage is only two and a half to one" (Haldane 1955). Many papers have been devoted to defining the conditions under which Hamilton's Rule holds (Michod 1982; Grafen 1991).

Our next reprinted article is by Orians (1969), who deals not with social interactions between relatives but with interactions between unrelated mating partners. Orians' paper and its immediate ancestors (Verner 1964; Verner and Willson 1966) ushered in a new period of field research on the mating systems of birds and other animals. The Orians paper was (and is) influential because it presents a model. Today models are taken for granted, but in 1969 they were unusual. Orians' paper presents no equations. Instead the model is delivered as a graph that communicates the essentials of the argument. The Verner-Willson-Orians model, and especially the Orians graph, enabled workers to grasp the connections (including tradeoffs) between territory quality, polygyny, and reproductive success. These variables (and some others) became the dominant issues in field studies in the decades that followed. For a discussion of models closely related to the Verner-Willson-Orians model, see Altmann et al. (1977) and Lenington (1980).

In the opening page of his paper, Orians (1969) refers to the Wynne-Edwards (1962) theory of population regulation. Wynne-Edwards' book caused a sensation at the time of its publication by viewing a huge array of social phenomena as adaptations to regulate population size.

For example, Wynne-Edwards argued that nesting colonies of seabirds performed raucous displays at dusk, in which the entire colony took flight and circled the nesting area, in order to access and regulate numbers. If too many birds participated in the display, so the argument goes, then some of the birds would curtail their own reproduction. Williams (1966) argued against Wynne-Edwards by pointing out that social regulation of numbers would be opposed by individual selection. Selection would act against individuals that curtailed reproduction. The Wynne-Edwards mechanism required selection at the level of groups. Colonies that regulated their numbers would not overeat their food supply and so might persist longer than colonies that did not practice self-regulation. Group selection acting at the level of the colony, however, would be opposed by individual selection. Williams argued that individual selection would overwhelm group selection and that, consequently, the kinds of group adaptations proposed by Wynne-Edwards were not plausible. In the years that followed, Williams' view prevailed but, at the time of Orians' (1969) article, the arguments put forward by Wynne-Edwards still had some proponents.

In a different approach to modeling selection and evolution, the Trivers (1972) paper reprinted here pioneered a new perspective on sexual selection. The Trivers paper appeared in a symposium commemorating the centenary of Darwin's 1871 book *The Descent of Man and Selection in Relation to Sex*. (As a lesson to symposium organizers, the paper by Trivers is the only one in the symposium that is routinely cited today, despite the fact that in 1971 he was a graduate student among a distinguished company of senior scientists.) Trivers took a fresh perspective. He drew attention to a new set of vari-

ables (variation in reproductive success, parental investment, good genes) and used graphical models to portray his arguments. The connections that Trivers drew between his variables were outlined in an intuitively appealing but largely verbal model. The graphs in his paper were cost-benefit functions from econometrics and were only loosely related to the verbal arguments. Aside from bringing a modeling approach, however loosely constructed, to sexual selection studies, Trivers (1972) also resurrected a forgotten but insightful paper by Bateman (1948). One facet of Trivers' argument, the cost of parental investment, has recently been reformulated by Arnold and Duvall (1994).

In the final paper reprinted in this section, Maynard Smith and Price (1973) introduced the concept of the evolutionarily stable strategy (ESS) and showed how it can be used to analyze animal contests. The approach pioneered in this paper led to a whole series of papers on animal contests, and to the application of the ESS concept to a broad range of evolutionary problems (Charnov 1982; Maynard Smith 1982). The ESS approach has been especially valuable for analyzing situations in which the fitness consequences of a particular action depend on the activities of other individuals in the population (e.g., sex ratio, sex allocation and sex change, sexual selection, parental investment and alternative strategies, sociality and cooperation). The paper opens with an easy-to-follow account of computer simulations and ends with the algebraic argument that became the standard in ESS models.

The models presented here on the evolution of social behavior, animal contests, mating systems, and sexual selection have utterly changed the way that we study these problems. Although the models admittedly were simplifications,

they allowed us to formulate testable hypotheses, to quantify important vari-

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