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I am submitting herewith a dissertation written by Harry Walter Greene entitled "Phylogeny, Convergence, and Snake Behavior." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.

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PHYLOGENY, CONVERGENCE, AND SNAKE BEHAVIOR

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DEDICATION

Whatever its lasting scientific merit, this dissertation represents a large part of four years of my life and the realization of a goal set almost 20 years ago. I affectionately dedicate both the merit and the effort to six people.

The late R. F. Ewer was an incredible woman, a paleontologist, comparative morphologist, ethologist, and above all, an unabashed lover of all animals. Griff's books provided knowledge, enjoyment, and a direction to my early interests in behavior; her letters are among my most prized possessions; and her forthright, indomitable style remains a source of inspiration.

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ABSTRACT

Comparative studies of snake behavior were used to confront three related conceptual issues in ethology: (i) Can behavior evolve? (ii) If so, how can the origins of similarities and differences in behavior among animals be assessed? (iii) What is the significance of this information for evolutionary biology?

Some workers have recently asserted that behavior does not evolve and that behavioral homologies are generally not discernible. A consideration of genetics and developmental biology suggests that both points of view reflect an unrealistic structure-function dualism. In a strict sense, only transcriptional products are genetically determined; all other aspects of the phenotype are dependent on epigenetic effects. At the molecular level, all aspects of the phenotype are variable, dynamic, and have an extended ontogeny subject to environmental influences. There clearly can be a relationship between nucleotide sequences in the genome and behavior patterns. These genes are subject to mutation, drift, selection, and gene flow. Behavior thus can evolve.

Chance, experience, homology, and convergence are best dealt with operationally as alternative hypotheses of resemblance that are potentially falsifiable by comparative and experimental studies. This requires samples of related and unrelated taxa that vary in potential experiential and selective constraints.

Constriction is an action pattern used for prey killing by at least 131 species of snakes in six families. Patterns of variation in four characters were used to describe the constricting behavior of

75 species. Twenty-seven species (13 genera) in the advanced family Colubridae exhibited intergeneric, interspecific, and individual variability in coil application movements. Each character state occurred in more than one taxon, and 19 patterns (based on combinations of character states) were observed. One or two patterns were usually consistent within a genus, but *Lampropeltis* was highly variable. *Boaedon*, *Elaphe*, *Pituophis*, and *Trimorphodon* used similar constricting behavior; *Arizona*, *Spalerosophis*, and *Spilotes* were distinct from these genera and from each other. Possible implications of these results for systematic studies are discussed.

Forty-eight species (26 genera) in the primitive families Acrochordidae, Aniliidae, Boidae, and Xenopeltidae usually used a single pattern, despite differences in prior experience, size, shape, habitat, and diet. This implies the shared retention of an action pattern used by their common ancestor. Since these taxa diverged no later than the early Paleocene, constriction must have been used as a prey killing tactic very early in the evolution of snakes. It is suggested that the oldest well-known snake, *Dinilysia patagonica* of the Cretaceous, was probably a constrictor, and that constricting was an ethological key innovation in the early evolution of snakes.

Defensive displays were compared among 124 species in five families of snakes. Type of defensive behavior was significantly associated with terrestrial or fossorial habits in genera with tail displays and genera with horizontal head displays, and with arboreal habits in genera with vertical head displays. The results of this comparison suggest that convergence has been widespread in the defensive behavior of snakes.

Taken together, these studies point to broader issues: What kinds of motor patterns are stable over long periods of evolutionary time? What kinds change rapidly and why? How are the rates and directions of change constrained by other factors? Rigorous comparative studies might provide answers to these and other questions regarding the evolution of behavior and the role of behavior in evolution.

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CHAPTER 1

INTRODUCTION

Unraveling the history of a phenomenon has always appealed to some people and describing the machinery of the phenomenon to others. In both processes generalizations can be made and tested against new information so both are scientific, but the same person seldom excels at both (MacArthur, 1972:239).

We can ask four basic questions about a behavior pattern (Tinbergen, 1963; Hailman, 1967): (i) How is it controlled? (ii) How does it develop in the individual? (iii) What is its function or selective advantage? (iv) What is its evolutionary and/or cultural history? In practice, particular studies and even whole disciplines tend to focus on one or two of these questions to the exclusion of others. For example, psychologists often seem most concerned with the first and second questions, and ecologists with the third. The fourth question, which deals with the evolution of behavior and emphasizes the comparative study of different taxa, provided an important impetus for the early work of European ethologists (e.g., Lorenz, 1941), but has received little attention in recent years. This may be due, at least in part, to the fact that behavior rarely leaves a fossil record and to the difficulties of determining homologies among the behavior patterns of different taxa (Atz, 1970). Another likely deterrent is the difficulty of studying enough taxa to permit testable generalizations about similarities and differences in behavior.

I feel that the problems involved in identifying homologous behavior patterns are overstated, and that the comparative study of behavior from a phylogenetic standpoint is both possible and important.

It has the potential to: (i) distinguish between the "phylogenetic origins of behavior (by finding similar responses in related species of differing ecologies) and the adaptive functions of behavior (by finding similar responses in unrelated species having similar ecologies)" (Hailman and Jaeger, 1974:758); (ii) suggest how and in some cases when a behavior evolved; and (iii) aid in understanding the acquisition of new and distinctive biological roles during the evolution of particular lineages of animals.

The approximately 2200 living snake species are excellent subjects for evolutionary comparative studies of behavior. Although they exhibit a variety of size-shape combinations and habitat preferences, all represent variations on a single structural theme: an elongate body, limblessness, and an extremely flexible jaw mechanism that permits the ingestion of large items without the assistance of mastication (Gans, 1961). This common *Bauplan* permits a limited number of behavioral solutions to ecological problems, such as feeding and defense against predators.

Most living snakes are usually assigned to either of two Superfamilies, the very old and morphologically primitive Booidea (boas, pythons, pipe snakes, and relatives), and the more recent and morphologically advanced Colubroidea ("higher snakes"). Each of these groups has an instructive fossil record, and has been subjected to systematic studies using a variety of anatomical, biochemical, karyological, and other characters (Dowling, 1975). Each group includes a diverse array of sizes (ca. .2-11 m total length in the Booidea, ca. .1-3 m total length in the Colubroidea) and ecological adaptations (terrestrial

aquatic, and arboreal in each). Finally, a practical advantage is that many snakes are easily maintained and observed in captivity, and zoological parks often keep synoptic collections of the world's snake fauna.

These attributes of snakes have not been widely appreciated, and most previous behavioral studies have consisted of isolated observations (e.g., Wright and Wright, 1957), preliminary surveys of particular postures and movements (e.g., defense, Mertens, 1946; Greene, 1973a), or experimental investigations of perceptual control (reviewed in Burghardt, 1970). Few topographic descriptions have been precise enough for comparative purposes, perhaps because these "legless tetrapods" lack the contentional anatomical reference points of most vertebrates. However, Greene (1973b) was able to develop a partial ethogram for the eastern coral snake, *Micrurus fulvius*. Other recent studies usually have concentrated on the motor patterns serving a particular function, such as feeding in water snakes (Drummond, 1977), courtship and mating in rat snakes (Gillingham, 1976), and intraspecific combat in pit vipers (Carpenter, 1977).

This dissertation uses comparative studies of snake behavior to confront three related conceptual issues in ethology: (i) Can behavior evolve? (ii) If so, how can we assess the origins of similarities and differences in behavior among animals? (iii) What is the significance of this information for evolutionary biology? Chapters 2 and 3 provide background essays on the rationale for comparative studies and the systematics of snakes. Chapter 4 describes the modal action patterns used for coil application by 75 species of constricting

snakes, and concludes that a single mode is homologous among 45 species in five primitive families. Chapter 5 examines ecological correlates of antipredator displays in 125 species of snakes and concludes that convergence has been widespread in the evolution of defensive behavior. Throughout, the approach has been to use explicit criteria for evaluating simple movement patterns and postures in a large, taxonomically and ecologically diverse sample of animals. Chapter 6 applies the results of the comparative surveys to broader problems of adaptive radiation in snakes, the role of behavior in evolution, and the evolution of behavior.

CHAPTER 2

DEVELOPMENTAL BIOLOGY, EVOLUTION, AND BEHAVIOR

. . . behavior is not a noun, defined and determined by a discreet locus on a DNA molecule. It is a process and derives from a series of interactions, some stochastic, some perhaps deterministic, which at times can achieve a certain level of predictability and stereotypy. . . . A *gene* refers to inheritable differences . . . it is nonsense to talk about the inheritance of behavior. . . (Klopfer, 1969a).

Ewer . . . [is] perpetuating a major misconception. "Behavior is something which an animal has got in much the same way it may have horns, teeth, claws, or other structural features," she writes . . . and this is where I take issue. The notion that behavior is a noun, a palpable entity, has been responsible for much of the nonsense that ethologists have uttered (Klopfer, 1969b).

Others--myself included--will be annoyed at the space given the topic of behavioral evolution, at the total expense of the opposing view that behavior does not evolve (Klopfer, 1975, in a review of Alcock, 1975).

I must insert a protest against a formulation whose original author I have not tried to trace but which has become increasingly fashionable . . . that what is genetically determined is the difference between one organism and another, a formulation which normally crops up in discussions of innate behavior and is supposed to show that the latter term is meaningless. The formulation is, however, perfectly idiotic: a difference is not a thing; it is the answer we get when we measure two things and subtract them. . . . A has inherited one set of genes which make it end up thus, while B has inherited another set which makes it end up otherwise. Nobody inherits the difference. Inheritance goes from parent to offspring, and the difference does not have any parents; it hasn't even got anywhere to live (Ewer, 1972, in a review of Hinde, 1970).

A. Introduction

A unifying theme of early ethological studies was that an animal's behavior is an evolved product of natural selection (Burghardt, 1973).

This notion persists, but there are some striking contrasts in the attitudes of recent authors regarding behavior and evolution. One

prominent ethologist has repeatedly asserted that behavior does not evolve (Klopfer, 1969a,b, 1973a,b, 1974, 1975), and another concluded that in any case we can rarely evaluate behavioral homologies (Atz, 1970). Among recent textbooks on animal behavior, Brown (1975) questioned the possibility of establishing behavioral homologies. Alcock (1975), Barash (1976), Eibl-Eibesfeldt (1970), and Wilson (1975) did not cite Atz (1970), but they sometimes discussed the behavior of extinct taxa or otherwise suggested that behavior does evolve.

This chapter provides a rationale for comparative evolutionary studies of behavior. It defines behavior with respect to other aspects of the phenotype, describes in broad terms the epigenetic pathway and its relationship to behavioral and morphological characters, and asserts that behavior can indeed evolve. The application of the concept of homology to behavior is discussed, and a methodology for evaluating similarities among the behaviors of different organisms is specified. Selected previous studies are used to illustrate the pitfalls and potentials for comparative analyses of behavior.

B. Behavior as a Phenotypic Parameter

Behavior includes fairly short-term neuromuscular, neurohormonal, and integrative responses of organisms to internal and external stimuli. This is not an exclusive definition, and I doubt that one is possible. Although most people's notions of what constitutes behavior are similar, the limits are probably arbitrary. I suspect that we usually (consciously or otherwise) categorize different aspects of an organism's

phenotype according to their duration as a continuous response (Fig. 1): exceptionally fast molecular events, such as enzyme-substrate reactions, are referred to as biochemical or physiological; somewhat slower responses are called behavior; and those features that appear stable over long periods, such as gross skin morphology, are known as structures.

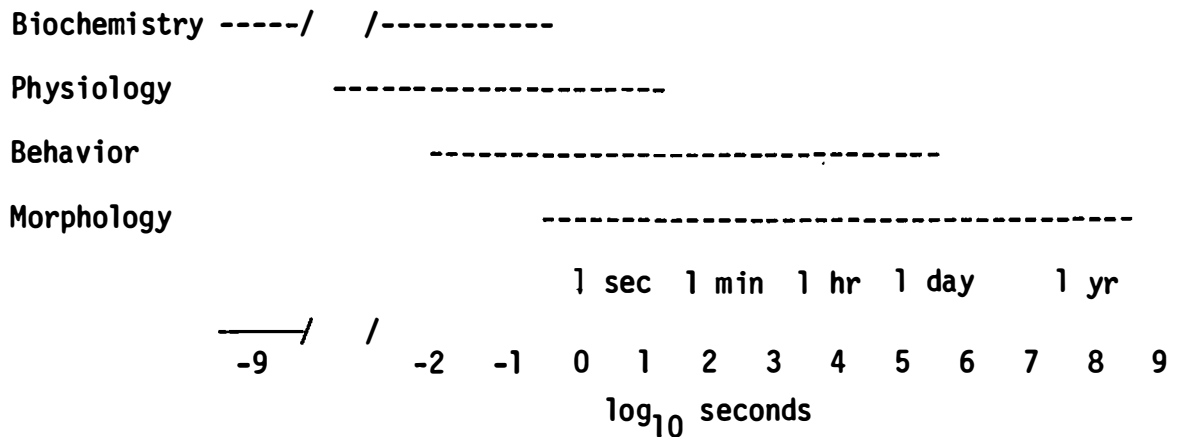


Figure 1. Phenotypic parameters and their durations as continuous responses.

In this study the concern is specifically with what are known in much of the ethological literature as fixed action patterns. Barlow (1968) suggested instead the term modal action pattern (abbreviated as MAP), and later "postulationally" defined a MAP as "(1) . . . a recognizable spatiotemporal pattern of movement that can therefore be named and characterized statistically. (2) It usually cannot be further subdivided into entirely independently occurring subunits, although some of its components may occur independently in other MAPs. (3) It is widely distributed in similar form throughout an interbreeding population. The definition stresses that the behavior is a normal part

of the biology of interbreeding individuals" (Barlow, 1977:95). Drummond (ms) pointed out that some behavior patterns are characterized by immobility. As a consequence Barlow's first point needs to be modified: a MAP can include (or be followed by another MAP that is) the resultant configuration of an animal's body and the maintenance of this posture. Defined as such, a MAP is a recognizable aspect of an animal's phenotype.

C. Developmental Biology of Behavior and Morphology

Development involves the proliferation, growth, migration, and differentiation of cells. For behavior, this encompasses all aspects of the receptor-effector systems, including endocrine secretions and their receptors, the central and peripheral nervous systems, sensory receptors, and the musculoskeletal system. Obviously development requires complex interactions between the organism and its environment (for general coverage of the biochemical and cellular bases of development, see Berrill and Karp, 1976). At the molecular level, five points need emphasis (for details see Curtis, 1975, and Gurdon, 1974):

- (i) Genes consist of nucleotide sequences in DNA molecules. (ii) These genes transcribe specific messenger RNA molecules (the "transcriptional products"), which in turn code for proteins or regulate other genes.
- (iii) Proteins are directly responsible for some cell structures; indirectly (via catalytic enzymes, transport molecules, etc.) they mediate many, if not all, cellular structures and functions. (iv) The proper structure and function of particular cells at particular times is dependent on the activation of certain genes and repression of others in the genome. (v) This regulation of gene activity is sensitive to intracellular and extracellular feedback.

Because the concern here is with motor patterns and resultant postures, and because I believe that the arguments of Klopfer (e.g., 1969a) and Atz (1970) are misstated in terms of the relationships among genes, behavior, and morphology, my statement begins with a brief consideration of neuromuscular embryology. The current state of the art can be summarized in terms of three controversial areas (Gottlieb, 1973a): theories of epigenesis, sources of embryonic motility, and the origins of neural specificity.

Predetermined epigenesis means that "the development of behavior . . . can be explained entirely in terms of neuromotor and neurosensory maturation" and that "factors such as the use or exercise of muscles, sensory stimulation, mechanical agitation, environmental heat, gravity, etc., play only passive roles in the development of the nervous system" (Gottlieb, 1973b:9). The basic point is that structure determines function, and not vice versa. Probabilistic epigenesis holds that "function not only facilitates neural maturation and behavioral development but that it [function] is capable of exerting a determinative influence as well" (Gottlieb, 1973b:11). The probabilistic attitude thus emphasizes a bidirectional structure-function relationship in development. The literature suggests that extremes of either viewpoint are not supported by the evidence, that there is variability within and among the components of different systems, and that the important problem is to identify the determinative and facilitative precursors of behavior in the development of different systems (Gottlieb, 1973a, 1974, 1976; Burghardt, 1977).

The embryonic motility issue has two components: (i) Whether or not early movements are "autogenous" (generated in the interneurons

and/or motor neurons), or if they are initiated by interoceptive, exteroceptive, or proprioceptive sensory stimulation. (ii) Whether or not the levels and patterns of early movements contribute to later behavior patterns. The answers to both questions appear to be, "yes, sometimes." According to Gottlieb (1973b:16) "the evidence taken together . . . indicates that embryonic motility is in a very basic and primary sense self-generated" but that (in some cases at least) it is also subject to "transient inhibitory and excitatory modulation by sensory and mechanical factors." A recent study by A. Bekoff et al. (1975:1245) is relevant to this issue. They observed simultaneous firing of synergistic muscles and alternate firing of antagonists in 7-day chick embryos, and concluded that "Since these patterns appear prior to the time at which motor responses to sensory stimulation . . . can be demonstrated, it is likely that the neural pattern-generating circuits for selective activation of muscles are established in the central nervous system without reliance on functional reflexes." There is thus good evidence that motor patterns in vertebrates can result from genetically determined patterns of neuromuscular connections, and that such movements can occur in typical form the first time the animal encounters an appropriate stimulus (Gottlieb, 1976:330).

The central problem of neural ontogeny is specificity: what controls the migration, differentiation, growth, and particular connectivity of neural cells? Gottlieb (1973) discussed three possible, non-exclusive answers. The electric field hypothesis states that electrical potentials in nerve tissues exert a directional effect on

the growth of nerve fibers. Outgrowing nerve fibers *in vitro* extend parallel to and in the direction of a current, but it is not known to what extent, if any, this approximates the *in vivo* situation. The discovery of electrochemical coupling of cells suggests that some variant of this idea deserves further study. The contact guidance hypothesis is based on observations that growing nerve fibers follow physical parameters (e.g., channels) of the growth environment, but fails to account for long-distance movements. The chemoaffinity hypothesis is that "nerve cells (and their fiber types) have a distinctive biochemical (cytochemical) composition that is matched only by cells and fibers in some other parts of the system and, because of these cytochemical identifies, synapses are formed between these particular cells and not other cells" (Gottlieb, 1973b:25-26; summarizing Sperry, 1965). Gottlieb (1973b) suggested a tentative synthetic view: that nerve fibers grow along existing mechanical structures, that bioelectrical effects impart some directionality over relatively long distances, and that specific chemoaffinities between cells determine which fibers terminate where.

Jacobson's (1974) "theory of neural plentitude" is consistent with the available evidence and attempts to reconcile earlier explanations for neural specificity and plasticity. Two types of neurons and two types of ontogenetic processes are central to his proposal. Macroneurons with long axons comprise the primary afferent and efferent pathways of the nervous system. They mature early in embryology and appear to be under a very "tight temporospatial pattern of genetic control." Microneurons are small interneurons with integrative functions, mature relatively late, and seem to be under lax genetic

control. Survival of particular microneurons among an initial "plentitude" presumably results from sensory and/or hormonal stimulation, and the final microneuron population results from "functional validation or deterioration." Jacobson's theory suggests distinct bases for predetermined and probabilistic epigenesis of neural specificity.

Some critics, while correctly ridiculing the notion of a behavioral homunculus (e.g., Klopfer, 1969a), seem to assume that "structural" characteristics such as bone and skin *are* strictly specified in the genome. Three studies will illustrate the fallacy of this attitude. Various osteological features (e.g., size and shape of individual bones, cranial crests, etc.) are typically used in vertebrate systematics, usually without consideration of the possible role of epigenetic factors in their formation. Yet Hollister (1918) compared the skulls of adult wild and zoo-raised lions and showed that different diets strongly affected the final size and shape of certain skull characters. DuBrul and Laskin (1961) surgically removed a small, cartilaginous plate (the spheno-occipital synchondrosis) from the base of the skulls of young rats. As adults the experimental animals exhibited altered skull morphology in comparison to normal rats, including not only the size and shape of individual bones but also gross shape of the entire cranium. The most salient difference between two species of European fire-bellied toads is that wild individuals typically have either bright yellow (*Bombina variegata*) or orange (*B. bombina*) ventral coloration. Recent studies by Bennett et al. (1974) suggest that these species differ in their capacity to

incorporate a dietary carotenoid into the belly pigment, rather than in genes for belly color *per se*. The presence of orange pigment (a structural characteristic) in wild *B. bombina* is therefore dependent on the action of particular genes in concert with a particular extrinsic factor. These studies and others (cf. Manning, 1975; Barlow, 1977) support the conclusion that MAPs can be genetically "determined" in the same way as are morphological characteristics.

D. Behavior and Evolution

Natural selection of the character states themselves is the essence of Darwinism. All else is molecular biology (Lewontin, 1972:182).

Klopfer (1973a and elsewhere) asserted that behavior does not evolve because it is a process, not a structure, and because it results from complicated probabilistic interactions between gene products and the environment. Such a process, he argued, cannot evolve in the sense that morphological characters do. A similar structure-function dualism underlies the arguments of Atz (1970). Hailman (1976a:194) subscribed at least partially to this dichotomy: ". . . behavior has a *kind* [my emphasis] of variability unknown in morphology. The length of a bone can be measured repeatedly and a frequency distribution of measurements obtained that relate to inherent problems of measurement. The same problems apply to measuring some variable in the motion picture of a fixed action pattern. However, if the same variable is measured in repeated performances of the 'same' fixed action pattern of a given individual animal, the variability in the measurements increases because there is a source attributable to difference among repeated performances. . . ."

Our current knowledge of developmental biology does not support a qualitative distinction between morphology and behavior in terms of their genetic bases or the kind of variability they exhibit. It is important to note that an isolated bone in a museum is not part of a living organism, but rather a more or less static collection of inorganic salts that "shadows" the phenotype of the bone in a live animal. The continued presence and characteristics of the bone in a living animal result from dynamic developmental and maintenance processes. Thus a structure can also be described as a "performance," albeit usually a continuous one; the antlers of deer, the feathers of birds, and the uterine mucosa of mammals with a menstrual cycle provide examples of "repeated performances" in structural characters. Were we to measure a bone repeatedly in a living animal, we would be sampling a *kind* of variability that is present in other aspects of the phenotype, including behavior. The characteristics of a bone can be usefully compared with a termite nest, which is a collection of inorganic materials with a predictable form and results from a series of complex social behaviors in a termite colony. The point is that bones and termitaria are the products of ongoing processes in living organisms.

In fact, what we *call* behavior is an outcome of a variety of processes. These processes and the developmental mechanisms that precede them result from the interactions of genetically coded transcriptional products with environmental variables. However, recall that what we *call* the structural aspects of the phenotype are *also* the outcome of processes (often continuous, e.g., epidermal differentiation), *also* based on complex epigenetic mechanisms, and *also* dependent on

the presence of the "predicted" environment for "normal" expression (cf. Gans, 1974; Løvtrup, 1974; Frazzetta, 1975a; and the studies on lions, rats, and frogs cited above).

We can now return to the question, Does behavior evolve? Evolution is generally defined as change in gene frequencies in a population (Mayr, 1970). A more realistic definition incorporating recent discoveries on gene regulation and population genetics (Lewontin, 1974) would be a change in the frequencies of groups of interacting genes. Clearly there is a relationship, sometimes quite specific, between the nucleotide sequences in the genome and the developmental mechanisms leading to an organism's phenotype, including those aspects of the latter that we call behavior. The frequencies of such genes can change as a result of maturation, drift, selection, and gene flow (see Ehrman and Parsons, 1976, for a review of behavioral genetics). I conclude that behavior can and very likely has evolved.

E. Comparative Evolutionary Studies of Behavior

Tinbergen's (1942, p. 48) statement that "movements of limbs, etc. can be measured just as well as the form of a structure" seems like whistling in the dark. . . (Atz, 1970:56).

. . . I expect that most ethologists will continue to whistle (Hailman, 1976b:194).

The goal of comparative ethology is to produce the most accurate estimate possible of the behavioral aspects of organic evolution (a paraphrase of Pang et al., 1977:372, in reference to comparative physiology). The central problem for such research is to evaluate the meaning of similarities and differences among the phenotypes of organisms. Three types of evidence have been used for evolutionary studies

of behavior: (i) Structural correlates of the behavior of extant taxa are examined in extinct forms. Examples include the head ornaments of certain dinosaurs, presumably used during intraspecific social encounters (Hopson, 1975), and the surface relief of cranial endocasts, which are known to reflect certain functional capacities (Radinsky, 1968). (ii) Artifacts of behavior. Examples include the trackways of dinosaurs (Ostrom, 1972) and bore holes left in the fossilized prey of predatory gastropods (Berg and Nishenko, 1975). (iii) Comparative analyses of modern forms. Methods (i) and (ii) establish structural and artifactual correlates of behavior in living animals, then assume that equivalent relationships exist between the unknown behavior and fossil remains of extinct species. Rigorous studies using method (iii) have been infrequent in recent years; the most impressive exception of which I am aware is Burt and Hailman's (in press) study of head scratching in parulid warblers.

The concepts of homology and convergence are central to comparative studies. Homology originally referred to similarities among structures, but soon included the assumption that the similarity resulted from evolutionary continuity among ancestors and descendants (for extensive discussions of the history and meaning of the term, see Atz, 1970; Campbell and Hodos, 1970). Some authors have suggested that the word homology might not be appropriate for behavior, either because of confusing vagaries of definition (Hailman, 1976b; Beer, 1977) or because of qualitative differences between behavior and morphology (Atz, 1970). Gans (1969) preferred to restrict the term to evolutionary similarities among structures, for reasons of clarity and historical precedence, but (pers. comm.) believes that the notion of

phylogenetic continuity is appropriate to behavior. None of these authors has suggested a substitute term for the phenomenon under consideration, and I believe that it will continue to be useful to speak of behavioral homology if the meaning is explicit. I suggest the following definition, modified from a more general form in Campbell and Hodos (1970:358; see also Hailman, 1976b, for an extensive and penetrating discussion): behavior patterns are homologous if they could, in principle, be traced through evolutionary lineages to a common precursor. Convergence has not been fraught with such semantic difficulties: it is the independent evolutionary acquisition of similar characteristics as a result of similar selective constraints (Mayr, 1970; Hailman, 1976b).

Campbell and Hodos (1970) discussed the kinds of evidence that have traditionally been used to identify homologous morphological characters: (i) The fossil record. Ideally, the most direct evidence would be if a trait occurs in fossil lineages that converge in time to a common ancestor. In practice, this situation rarely if ever obtains (cf. Atz, 1973). It is worth noting that most living species do not have known close fossil relatives, and that those that do are usually represented by only the "hard" parts of their phenotypes. (ii) Minuteness of similarity. Presumably the more closely characters resemble each other in different taxa the more likely they are to be homologous. (iii) Multiplicity of similarities. (iv) Ontogenetic similarity. Since developmental patterns are to some degree inherited, they might also be used to determine homology. Criteria (ii), (iii), and (iv) fail to exclude convergence.

Most attempts to distinguish behavioral homologies have used the criteria developed by morphologists (e.g., the treatments of behavioral homology by Baerends, 1958; and Wickler, 1961). Atz (1970) provided a thought-provoking and influential critique of these and other applications of the concept of homology to behavior. He concluded that motor patterns might indeed be homologous, but that it is generally not possible to operationally distinguish such cases because of what he viewed as fundamental differences between behavior and morphology. I agree with Atz that the essential defining criterion should be derivation from a common ancestral character state, that homologous character states need not be controlled by homologous genes, that ontogeny cannot be a decisive determining criterion (see also DeBeer, 1958), that correspondence with particular structures cannot be an essential basis for determining homologies, and that there is very rarely fossil evidence for a particular behavior pattern. Each of these statements also applies to morphological features.

A two-part distillation of the remainder of Atz's critique and my response follows:

(i) "Behavior is much more difficult to treat comparatively than is structure because of its variability, continuity, extended ontogeny, and the evanescence of each behavioral act" (Atz, 1970:69). These aspects of behavior also apply to structures (see pp. 13-15 above), and *a priori* dogmatism concerning their relative impact on the determination of homologies can only stifle further studies.

(ii) "Convergence in behavior is prevalent, probably because of intense selection pressures and limited possible responses by the animal" (Atz, 1970:69). This is certainly true in many cases (Wilson,

1975), but it is also true of complex morphological features (e.g., Lombard and Wake, 1976). As a strict apriorism this attitude can only retard attempts to separate convergence and homology.

Atz (1970) concluded that very similar behavior patterns in closely related forms are probably homologous, and Eibl-Eibesfeldt (1970) suggested this as an "auxilliary criterion" for assessing behavioral similarities. The assumption here seems to be that it is more parsimonious to assume that similar behaviors in related taxa are homologous rather than that they are independently derived. This may be more satisfying intellectually than a totally unsupported speculation, but not very much more. Moreover, there is no reason to assume that evolution has always been parsimonious (Hecht, 1976). A potentially more fruitful approach is to conduct comparative studies within the framework of explicit alternative, refutable hypotheses.

Most contemporary morphologists probably conclude that "resemblances are homologous in the absence of contrary evidence" (Ostrom, 1976). In contrast, Gans (1974:17) suggested that "In operational terms, demonstration of homology *requires* [my emphasis] that the observed similarity be greater than random and not due primarily to contemporary selective influence." The discussions of Zeigler (1973), Gans (1974), Hailman and Jaeger (1974), and Hailman (1976b) suggest that comparative studies can distinguish among four possible origins of similar behavior. This approach has been referred to as "ecological algebra" by Zeigler (1973:130), briefly articulated by Hailman and Jaeger (1974, quoted on pp. 1 above), and formalized as a parametric research design by Hailman (1976b:Table 2, see Table 1 here).

Table 1. Ideal Design for Comparative Studies of Behavior

Phylogenetic Relationships	Selective and Experiential Factors	
	Similar	Dissimilar
Close	A	B
Distant	C	D

Modified from Hailman (1976a:Table 2). A through D represent samples of species to be studied.

The working assumption is that there are four possible origins of similar phenotypes in different organisms: (i) Chance; (ii) similar experiential factors in the lives of individual animals; (iii) convergence; and (iv) homology. It is difficult to directly test for the last possibility without a continuous fossil record, but (i), (ii), and (iii) can be refuted by comparative studies. Chance becomes rapidly less likely as more species are involved; similar behavior patterns in unrelated species with similar selective constraints should be attributed to convergence; the effects of experience can be evaluated within and between individuals; and similar behaviors in related species that vary in relevant aspects of ecology, individual experience, and morphology can be attributed to common ancestry.

Finally, a word about classification. It is now generally agreed that a conclusion that two taxa are more closely related to each other than to a third taxon must be based on resemblance due to common ancestry. Furthermore, retained primitive characteristics are not useful for distinguishing members of one group from those in another group if the two groups share a common ancestor that also

exhibited the primitive characters. For example, in the upper diagram of Figure 2, taxon 4 is more closely related to 3 (its "sister group") than it is to 2, because it shares a more recent common ancestor with 3. Note, however, that 4 resembles 2 more than 3 because 4 and 2 retain a primitive state (A'), as determined by comparison with taxon 1 (an "outgroup"). Only similarities unique to the group in question can be used to distinguish it from other related groups. In the lower diagram of Figure 2, taxon 4 is more closely related to 3 (its sister group) than it is to 2, because it shares a more recent common ancestor with 3. This relationship is indicated by the shared derived state (A') found in 3 and 4. Taxon 2 retains the primitive state (A), as determined by comparison with taxon 1 (an outgroup). Therefore, the use of behavioral characters in testing hypotheses of relationship requires that (i) alternative sources of resemblance be evaluated and that (ii) the polarity (i.e., primitive versus derived) of the character states be determined (for detailed discussions of these points, see Eldredge and Tattersall, 1975; Hecht, 1976; Kluge, 1977).

F. Comments on Previous Studies

To date few comparative studies of behavior have framed questions of similarity in a refutable fashion, or evaluated the polarity of character states. Four studies will illustrate the necessity for and the utility of an operational approach.

Sears et al. (1976) used six motor patterns and one vocal display to argue for certain relationships among members of the avian suborder Lari (gulls, terns, skimmers, and others). They mentioned

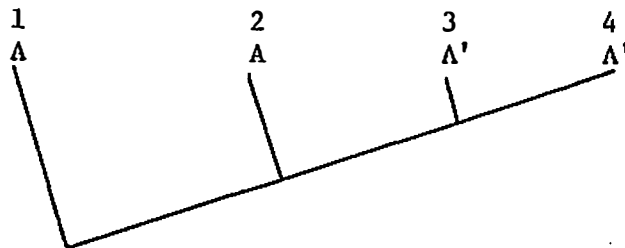
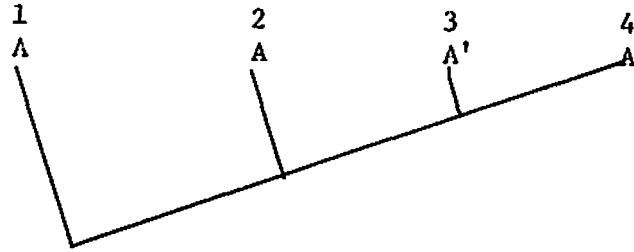


Figure 2. Outgroup comparison, determination of character state polarity, and phylogenetic relationships.

homologies with respect to three displays and non-homologies between two others. The criterion in each case was evidently similarity, although in only one instance (two non-homologous motor patterns) was this clearly stated. Since other possible sources of similarity were not evaluated, their conclusions are at best tenuous.

Moynihan (1973:8) postulated that behaviors in certain squids and octopi are homologous on the basis of strong similarity: ". . . at least four major displays are both extremely complex, exaggerated, and 'unexpected,' yet strikingly similar in many details (of causation and function as well as form) in the various species. These displays would appear to have been ritualized before the lines diverged . . . most probably in the late Triassic. . . . the patterns are [thus] not only old but also have been remarkably conservative during evolution." This appears to be a case where the hypothesis of homology could be operationally tested if information on the ecologies, morphologies, and ontogenies of the cephalopods were available.

Dewsbury (1975) studied the copulatory behaviors of 31 species of muroid rodents, and defined 16 possible patterns based on the presence or absence of copulatory locks, thrusting, multiple ejaculations, and multiple intromissions. The rodents that he studied exhibited a diversity of ecologies and reproductive morphologies, and copulatory patterns correlated more closely with anatomical and ecological factors than with phylogeny. Dewsbury's study was somewhat exceptional in that he explicitly falsified the hypothesis of homology. In doing so, he demonstrated that copulatory behaviors in these animals have been repeatedly and independently subjected to similar selective pressures.

M. Bekoff et al. (1975) applied multivariate statistical techniques to behavioral data for infant coyotes, wolves, dogs, and "New England canids." Their analysis demonstrated that the latter, thought to be hybrids between dogs and one of the two wild species, were behaviorally more similar to coyotes than to wolves. This result accorded well with a similar analysis of morphological characters, and M. Bekoff et al. (1975:1224) viewed their studies as indicating that "quantitative analysis of behavioral characters are useful in deriving taxonomic relationships." Most biologists prefer that taxonomy reflect genealogical relationships rather than just phenetic similarities. While I expect that M. Bekoff et al.'s conclusions regarding the New England canids are correct, the application of behavioral data to classification ultimately requires an assessment of the origins of similarities and of the polarities of character state transformation.

G. Concluding Remarks

I have argued in the first part of this chapter that behavior can be genetically determined, at least to the extent that any aspect of the phenotype beyond the level of transcriptional products can be "determined." It follows that behavior does evolve, contrary statements notwithstanding. In the second part of the chapter, a method is specified for distinguishing among possible origins of similar behavior patterns in different taxa, and the rules for applying behavioral data to classification are stated.

CHAPTER 3

SNAKE CLASSIFICATION AND EVOLUTION

A. Introduction

Three major groups of snakes are generally recognized, here referred to as the Superfamilies Typhlopoidea (blindsnakes), Booidea (primitive snakes), and Colubroidea (advanced snakes). The typhlopoids are a highly aberrant assemblage of blind burrowers; to my knowledge they do not constrict prey, and are not discussed further here. The summary of the classification and evolution of snakes that follows is prerequisite to the discussions of snake behavior in Chapters 4, 5, and 6.

B. Classification, Origin, and Radiation of Primitive Snakes

The classification of primitive snakes used here (Figure 3) follows Bellairs (1969) with minor modifications; my rule of thumb has been to treat taxa as distinct and equal in taxonomic rank whenever relationships among them are in doubt. I follow McDowell (1975) and Rieppel (1976) in treating the Xenopeltidae as a separate family, rather than as a subfamily of the Aniliidae (Bellairs, 1969) or the Boidae (Underwood, 1976). *Loxocemus* is placed in a separate subfamily of the Boidae, rather than in the Pythoninae (Bellairs, 1969; Frazzetta, 1975b) or Xenopeltinae (Underwood, 1976) or the Boidae, or as a separate family more closely related to aniliids than to boids (McDowell, 1975). The Bolyeridae are treated as a family (McDowell, 1975; Dowling, 1975), rather than as a subfamily of the Boidae (Bellairs, 1969) or the

- Superfamily Booidea (primitive snakes)
 - Family Aniliidae (pipe snakes)
 - Family Acrochordidae (wart snakes)
 - Family Boidae
 - Subfamily Boinae (boas)
 - Subfamily Calabariinae (African burrowing python)
 - Subfamily Erycinae (sand boas)
 - Subfamily Loxoceminae (dwarf python)
 - Subfamily Pythoninae (pythons)
 - Family Xenopeltinae (sunbeam snake)
 - Family Tropidophiidae (dwarf boas)
 - Family Bolyeriidae (Round Island boas)
 - Family Uropeltidae (shield-tailed snakes)
- Superfamily Colubroidea (advanced snakes)
 - Family Colubridae (colubrid snakes)
 - Family Elapidae (cobras and relatives)
 - Family Hydrophiidae (sea snakes)
 - Family Viperidae (vipers, pit vipers)

Figure 3. A classification of snakes. (See Chapter 3 for details.)

Tropidophiidae (Underwood, 1976). I follow Dowling (1975), McDowell (1975), and Underwood (1976) in elevating the dwarf boas to familial status as the Tropidophiidae, rather than including them in the Boidae (Bellairs, 1969). I follow Underwood (1976) in recognizing a separate subfamily for the African burrowing python, the Calabariinae. The genera and species of booid snakes recognized here generally follow Stimson (1969), Dowling (1975), and McDowell (1975; in press, a,b). I distinguish two genera of doubtful validity (McDowell, 1975), *Bothrocheilus* and *Morelia*, to emphasize minor radiations and the diversity of higher taxa that I sampled in the constricting survey. It is important to note that the precise familial, subfamilial, and generic placement of the species in the Booidea does not affect the conclusions reached in Chapter 4. It is sufficient that all studies support both their common ancestry and their distinction from the advanced snakes.

Comparative morphological studies of fossil and Recent forms indicate that primitive snakes evolved from an unknown lizard ancestor at least as early as the lower Cretaceous (Frazzetta, 1970), and perhaps during the Jurassic (Bellairs, 1972). There is evidence that the ancestors of snakes were most closely related to the lizard infra-order Anguimorpha (McDowell and Bogert, 1954), particularly the Superfamily Varanoidea (Bellairs, 1972; McDowell, 1972). The latter group includes the living families Helodermatidae, Lanthanotidae, and Varanidae, and the fossil families Aigialosauridae, Dolichosauridae, and Mosasauridae. Studies by McDowell (1972) suggest that among known lizards the fossil dolichosaurs and living *Lanthanotus* are most closely related to the ancestral snakes.

Most studies have concluded that aniliids are the most primitive living snakes (e.g., Bellairs, 1972; Estes et al., 1970). Among living taxa, they are morphologically the most similar to the oldest known fossil snake, *Dinilysia patagonica* of the Cretaceous (Estes et al., 1970); and they are widespread in the fossil record from the Cretaceous until the Miocene (Auffenberg, 1963; Estes, 1970; Tihen, 1964). However, recent anatomical studies led McDowell (in press a) to conclude that *Acrochordus* retains even more primitive (lizard-like) characters than *Dinilysia* or the aniliids, and the ancestor of *Acrochordus* diverged prior to all other living forms. Observations of tongue-flicking behavior in lizards, *Acrochordus*, and other snakes support this conclusion (Greene and Gove, in preparation)

Studies on the origin and radiation of early snakes have been evaluated and summarized by Underwood (1976). Boids apparently arose from an aniliid-like ancestor, and their radiation began during the

Cretaceous on the ancient supercontinent of Gondwanaland. Fossil boids are widespread in the early Tertiary but relatively rare after the Miocene. Among living boids, *Loxocemus* appears to be a survivor of proboid stock, and *Xenopeltis* is perhaps a specialized offshoot of the line that led to *Loxocemus*. Underwood (1976) concluded that a *Calabaria*-like snake was derived from such a proboid stock and gave rise to living pythons. He also suggested that the Tropidophiidae and Bolyeridae are descended from a common ancestor with the Calabarinae, and that these living families are Gondwanaland relicts. Underwood viewed the erycine boas as primitive to others, and concluded that the New World erycines (*Charina*, *Lichanura*) are more primitive than Old World sand boas. He also concluded that the radiation of large boas (Boinae) began prior to the breakup of Gondwanaland at the end of the Mesozoic. By the mid-Tertiary boids had disappeared from much of their former range, and today are largely restricted to the tropics. This distribution has been attributed to competitive exclusion by colubrids (Bogert, 1968), but in my opinion the evidence is circumstantial and fails to deal with alternative explanations.

C. Classification, Origin, and Radiation of Advanced Snakes

Classification of higher snakes is controversial, and the nearly 2000 species have been placed in as many as four families and 34 subfamilies (Smith et al., 1977). It appears that such extensive subdivision of higher categories is of little practical value at this point, because many genera (including most of those dealt with in my studies) have not been investigated in detail and therefore cannot be placed in any of the proposed subfamilies with confidence. For my purposes

it is convenient to recognize four families (Figure 2), with all of the advanced snakes that constrict placed in the Colubridae.

Colubroids evolved from an unknown, presumably booid, ancestor in the early Tertiary (Rabb and Marx, 1973) or even the late Cretaceous (Underwood, 1976). Fossil colubrids are known from the Eocene and Oligocene, elapids from the Oligocene, and viperids from the Miocene (Estes, 1970). In any case, the Colubridae did not achieve prominence in the fossil record until the Miocene (Tihen, 1964; Estes, 1970). Most modern groups probably differentiated during the latter epoch, and several Recent genera (e.g., the constrictors *Elaphe* and *Lampropeltis*) or their close relatives were present in the Pliocene. By the mid-Tertiary colubrids were widespread, and today they are the dominant family in the world's snake fauna (Estes, 1970; Rabb and Marx, 1973; Tihen, 1964).

CHAPTER 4

CONSTRUCTING BEHAVIOR

A. Introduction

Constriction is a prey capture technique in which an animal is immobilized by pressure exerted by two or more points on a snake's body. This behavior provides a good problem for comparative evolutionary studies for several reasons. It usually consists of a single, easily defined movement, and thus corresponds well with the ethological concept of a fixed or modal action pattern (Burghardt, 1973; Barlow, 1977). Its form varies interspecifically, and in some cases intraspecifically, individually, and ontogenetically. It is widespread in both primitive and advanced snakes, and each of these groups includes the necessary diversity of ecological and morphological adaptations for an assessment of similarities and differences.

Although there are at least 131 species of snakes that constrict prey (Table 2; Appendix A), this behavior has rarely been accurately described and its ontogeny, control, and evolutionary history have not been examined in detail. Pope (1961) and Frazzetta (1966) described certain aspects of the movements used by boids, and there have been short accounts on several species by other authors (Appendix A). The first comparative study dealt with six species of colubrids (Shrewsbury, 1969), and the only thorough motion picture analysis was recently completed by Greenwald (ms). A more recent survey dealt with 22 species of boids and 19 species of colubrids (Willard, 1977). These studies are critically evaluated in a later section of this chapter.

Table 2. Occurrence of Constricting Behavior in Snakes and the Scope of This Study

	Booidea					Colubroidea
	Acrochordiae	Aniliidae	Boidae	Tropidophiidae	Xenopeltidae	Colubridae
Genera						
in family	1	3	20	4	1	Ca. 400
known to constrict	1	1	19	4	1	41
studied	1	1	19	4	1	13
Species						
in family	3	Ca. 10	59	20	1	Ca. 1500
known to constrict	1	2	41	10	1	76
studied	1	1	38	7	1	27
Individuals	1	2	99	17	1	60
Observations	1	3	306	40	2	227

This chapter presents a comparative survey of the movements used for constricting coil application by 75 species of snakes in six families. It provides a descriptive framework for future studies of this behavior, and evaluates the patterns observed thus far on the basis of criteria discussed in Chapter 2.

B. Materials, Methods, and Descriptive Terminology

Live Animals

Live snakes were studied in zoos, private collections, and the Reptile Ethology Laboratories of the University of Tennessee. Zoo snakes were observed in their home cages. They were usually fed dead prey from forceps, but if a snake failed to constrict I requested that the keeper either offer it a live item or jiggle the dead prey. Snakes in my laboratory were fed in their home cages or in a special filming container. The filming cage had a trapezoid shaped bottom to prevent the snakes from hiding in a corner and was painted flat white. Snakes in the laboratory were always fed live prey, including rodents (mice, rats, hamsters), birds (domestic chickens, quail), frogs (*Hyla* sp., *Eleutherodactylus ricordi*), and lizards (*Anolis carolinensis*, *Xanthusia vigilis*). An attempt was made to feed each snake as many kinds of prey items as possible, but many fed only on either ectotherms or endotherms.

My remarks on the feeding behavior of anguimorph lizards are based on unpublished observations over the past seven years. These included representatives of the following taxa (number of individuals in brackets): Anguidae (*Abronia deppii* [1], *A. mixteca* [3], *Gerrhonotus gadovi* [2], *G. kingi* [1], *G. liocephalus* [6], *G. multicarinatus* [2],

Ophisaurus attenuatus [1], *O. koellikeri* [1]), Helodermatidae (*Heloderma horridum* [2], *H. suspectum* [2]), Xenosauridae (*Xenosaurus grandis* [4]), and Varanidae (*Varanus bengalensis* [1]).

Recording Methods

Some feeding encounters were recorded on 1/2 inch videotape at 60 fps with a portable Sony television camera and recorder. These tapes were examined in detail on a monitor with a stop-action switch and a slow-motion editor. Additional sequences of certain species were filmed with 8 mm color (Kodak Hi-Speed Ektachrome) or black and white (Kodak Tri-X) cine film, using either a Nizo S-80 or Beaulieu 4008 ZM II camera and movie light. Cine films were shot at 24 fps and analyzed frame-by-frame with a Lafayette Analyzer Projector. Some postures achieved during coil application were photographed with 35 mm color (Kodachrome 64) or black and white (Plus-X) film, using a single lens reflex camera with a 100 mm bellows lens and electronic flash.

After variables had been identified by viewing videotapes and cine films, I prepared a checklist of items to be noted during observations of constriction. This included basic information on the snake and its prey, and word lists of alternative outcomes for each variable. An example is provided in Appendix B. Using these checklists, I was able to quickly record the behavior of large numbers of snakes in my laboratory and during visits to zoos (see Appendix C for a list of species, individuals, and number of observations). Data on four species I was unable to observe were taken from a sequence of 35 mm still photographs of *Trachyboa boulengeri* (by B. Tryon), a sequence of 35 mm

still photographs of *Acrochordus javanicus* (by R. Honegger), and 8 mm color cine films of *Elaphe flavirufa* and *E. triaspis* (by J. C. Gillingham).

Definitions

A loop is defined as a portion of the snake's body that encircles a prey item once. A coil comprises all of the loops applied to the prey during one application movement.

General Phases of Feeding Behavior

The feeding behavior of snakes that I studied included five phases. Orientation and approach were accompanied by tongue-flicking, which presumably functions in chemoreceptive prey recognition (Burghardt, 1970). Prey was seized by a quick forward movement and either pinned against the substrate or lifted and turned about its long axis. Constriction began when body loops were applied to the prey and tightened. Preingestion movements included jaw movements to one end of the prey, or release of the prey and location of a site for swallowing. Swallowing utilized the alternate protraction and retraction of jaw elements that apparently characterizes all snakes (Gans, 1961); it was sometimes accompanied by the application of "post-constriction" loops that reduced the diameter of the prey prior to swallowing. This study was restricted to motor patterns used for immobilization during coil application to single prey items.

Variables in Coil Application

The descriptions of Pope (1961), Frazzetta (1966), and Shrewsbury (1969) and my initial analysis of videotapes and films suggested

that six variable aspects of coil application could be observed and characterized using checklists:

(I) Application movement. Two discrete movements were observed. During (1) winding (Fig. 4), the prey is turned about its long axis by the snake, so that anterior loops are applied like rope on a windlass (this metaphor was suggested by Shrewsbury, 1969). During (2) wrapping (Fig. 5), the prey is pinned to the substrate and one to several loops are applied over, under, and around the stationary prey by the snake. Some snakes used winding and wrapping in a single coil application, and this was recorded as (3) mixed.

(II) Initial twist. If the part of the snake's body that formed the first loop was rotated about its long axis as the first loop was applied (1), a twist was present (Figs. 4 and 6). This resulted in the snake's venter facing toward the prey's body or (if the twist approached 90°) toward the snake's head. If (2) no twist was present (Fig. 7), the snake's venter faced away from its head. Occasionally both states occurred in different loops of a single coil, and this was recorded as (3) mixed.

(III) Coil composition. Initially I recorded if the snake's anterior, middle, posterior, tail, or some combination (including all) of these portions comprised the coil (see Figs. 4-7). These categories were subsequently collapsed to (1) "anterior" (including anterior and middle), (2) "posterior" (including posterior and tail, and (3) "both."

(IV) Long axis orientation. An imaginary line passed through the long axis of the coil (i.e., perpendicular to the plane of the individual loops and usually parallel to the long axis of the prey), was

Figure 4. Constricting coil application in a wart snake, *Acrochordus javanicus* (Acrochordidae), illustrating the character state "winding." Note that the prey is rotated counter-clockwise between the upper and lower figures. Based on consecutive 35 mm photographs of a single coil application movement. (Copyright by R. Honegger, used by permission.)



Figure 4

Figure 5. Constricting coil application in a kingsnake, *Lampropeltis triangulum* (Colubridae), illustrating the character state "wrapping." Note that the prey's position is approximately the same in the upper and lower diagrams, and that a loop of the snake's body is being raised up and over the mouse. Based on consecutive 35 mm photographs of a single coil application movement.

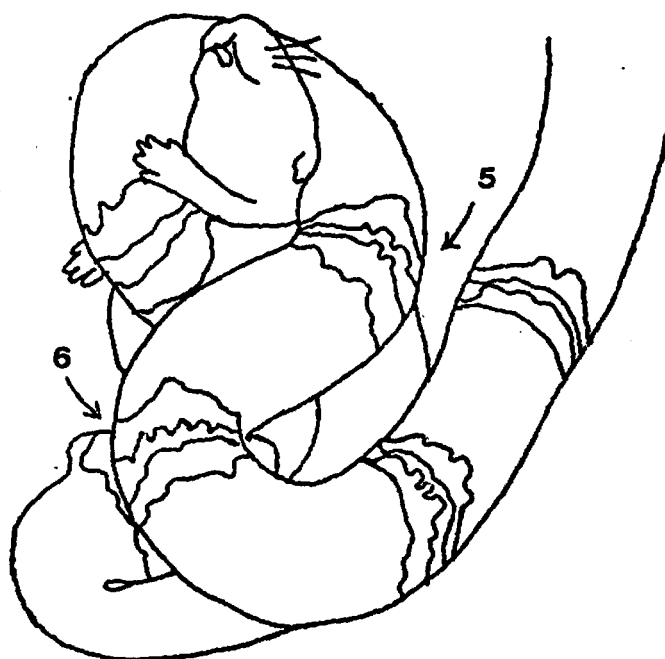
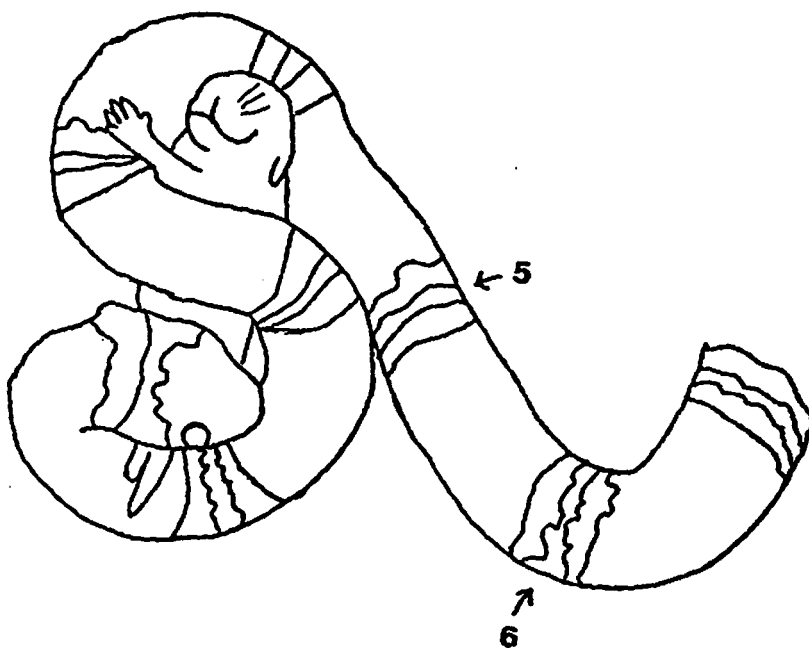


Figure 5

Figure 6. Constricting coil application in a dwarf boa, *Tropidophis canus* (Tropidophiidae), illustrating the character states "twist" and "horizontal." Note that the snake's ventral scales face toward its head.

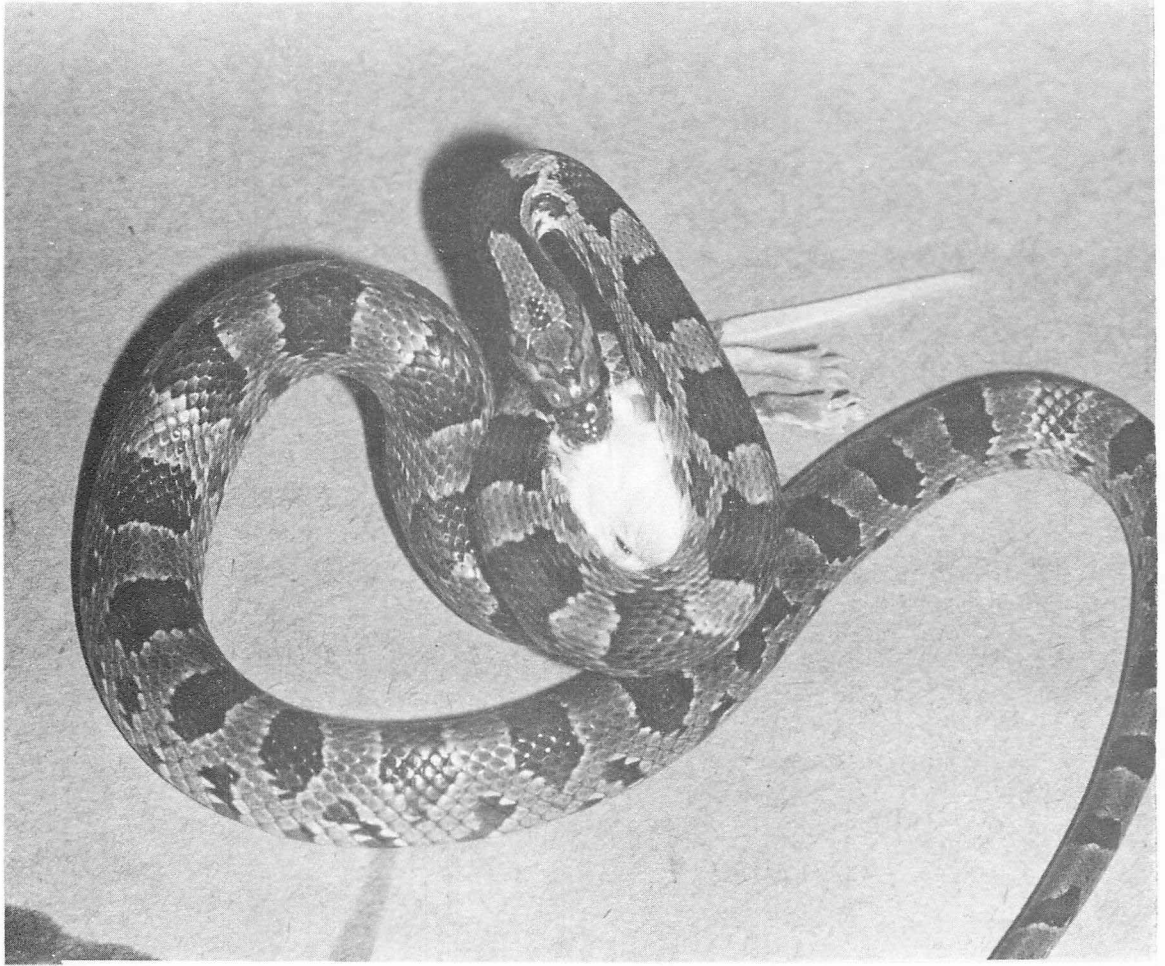


Figure 6

Figure 7. Constricting coil application in a corn snake, *Elaphe guttata* (Colubridae), illustrating the character states "no twist" and "vertical." Note that the snake's scales face away from its head.





Figure 7

parallel to the substrate (termed [1] horizontal, Figs. 4-6), perpendicular to the substrate (termed [2] vertical, Fig. 7), or at some intermediate angle (termed [3] angled). In some cases combinations of these states (4-6) occurred during a single coil application.

(V) Aspect of body used. The portion of the snake's body applied (i.e., adjacent) to the prey was either the right or left lateral, the ventral, or some combination of these surfaces. This character was not used to describe patterns of application movements for two reasons: (i) individual snakes varied in the use of right and left lateral surfaces, and a preliminary study by D. Sonntag (unpublished) showed that this was not related to the prey's direction of approach; (ii) whether the lateral or ventral surface is applied to the prey reflects whether or not a twist is present, so that this character repeats (II).

(VI) Number of loops. I defined the beginning of a loop as the anterior most point on the snake that touched the prey and the end of a loop as the adjacent point on the next posterior encirclement of the snake's body. The number of loops was visually estimated and recorded on the checklist in 1/2 loop intervals. A preliminary study (Greene and Weldon, unpublished) showed that the number of loops was correlated with prey weight in several colubrids but not in boids. Since this character was more or less constant in the Booidea (ca. 1.5 loops per coil) and covaried with an extrinsic factor (prey weight) in colubrids, it was not used to describe patterns of coil application.

Patterns of Coil Application Movements

Combinations of the 15 states for characters I through IV generate 162 possible combinations or patterns (Scheme 1, Appendix D), and 5/6 of these resulted from variation among the six states of character IV. I eliminated this character for the initial description of pattern variation because (i) it varies substantially within individuals for which there are repeated observations (Table 3); (ii) the states are arbitrary points on a continuum of long axis angles; and (iii) I have doubts about the accuracy with which I distinguished "horizontal" and "vertical" from "angled" in some cases. The remaining characters (three states each) generate 27 possible patterns (Scheme 2, Appendix E).

Statistics

Most measures of variability used for behavior are not appropriate for nominal variables (cf. Barlow, 1977), and thus could not be applied to the coil application character states or their combinations. I used V , the percentage of non-modal states, to assess variability within characters and among patterns within each taxon. For comparisons across a set of taxa, a weighted average percentage (A_w) of non-modal states was calculated (Vorisi, 1971:443):

$$A_w = \sum_{j=1}^n V_j S_j / S_n$$

where V_j is the percentage of non-modal states for a subset (i.e., genus), S_j is the number of observations for the subset, and S_n is the total number of observations in the set. A_w is expressed as a decimal fraction.

Table 3. Distribution of Character States for 26 Genera of Primitive Snakes.

Taxa	I				II				III				IV						
	(1)	(2)	(3)	V	(1)	(2)	(3)	V	(1)	(2)	(3)	V	(1)	(2)	(3)	(4)	(5)	(6)	V
Acrochordidae																			
<i>Acrochordus</i>	1			0	1			0	1			0	1						0
Aniliidae																			
<i>Cylindrophis</i>	2			0	3			0	3			0	2	1					.33
Boidae																			
<i>Acrantophis</i>	3			0	3			0	3			0	3						0
<i>Aspidites</i>	2			0	2			0	2			0	1			1			.50
<i>Boa</i>	29			0	28	1		.03	24	1	1	.08	20	1	3				.17
<i>Bothrochilus</i>	2			0	2			0	2			0	1			1			.50
<i>Calabaria</i>	7			0	7			0	7			0	4		2	1			.43
<i>Candoia</i>	8		2	.20	10			0	10			0	10						0
<i>Charina</i>	1			0	1			0	1			0	1						0
<i>Chondropython</i>	7			0	7			0	7			0	5	1					.17
<i>Covalius</i>	22			0	22			0	22			0	17	1		1			.11
<i>Epiplatys</i>	143	3		.02	146	10	2	.08	154	2		.01	128	16	9	1	1		.17
<i>Eryx</i>	4			0	4			0	4			0	2		1			1	.49
<i>Eumactes</i>	24			0	24			0	24		1	.04	18	3	1		1	1	.25
<i>Gongylophis</i>	1			0	1			0	1			0	1						0
<i>Liasis</i>	10		1	.10	10			0	11			0	7	3	1				.36
<i>Lichanura</i>	1			0	1			0	1			0	1						0
<i>Loxocemus</i>	11			0	11			0	11			0	10	1					.09
<i>Moralia</i>	1			0	1			0	1			0	1						0
<i>Python</i>	19			0	18		1	.05	18			0	16			1			.06
<i>Saiaia</i>	2			0	1			0	2			0	2						0
Tropidophiidae																			
<i>Exiliboa</i>	1			0	1			0	1			0		1					0
<i>Trachyboa</i>	2			0	2			0	2			0	1				1		.50
<i>Tropidophis</i>	34		4	.03	35			0	35			0	31	1	1	1	1		.11
<i>Ungaliophis</i>	1			0	2			0	2			0	1						0
Xenopeltidae																			
<i>Xenopeltis</i>	2			0	2			0	2			0	2						0
Totals	340	3	4		344	11	4		353	3	1		286	28	19	7	4	2	

V = percentage of non-modal states.

I used a measure of stereotypy (the inverse of variability) to assess variability across characters within and between taxa. Stereotypy, following Riechert (ms) is given by:

$$S = \frac{2w}{O+E}$$

where w is the minimum sum of the frequencies of states in common between the expected and each observation (i.e., the sum of the expected frequencies for each state observed in a particular coil application event), E is the average frequency of each state for all observations, and O is the sum of the frequencies of all states for each observation. I calculated S for all individuals, species, and genera represented by three or more observations. In each calculation, E was based on all observations for the sample being considered. For example, stereotypy for an observation by an individual *Lampropeltis triangulum* was calculated against different E values for the individual, the species, and the genus. Paired comparisons of S values for different samples were checked for significance with Mann-Whitney U tests (Snedecor and Cochran, 1967).

The frequencies of Scheme 2 patterns were compared among genera using the Coefficient of Similarity (Curtis, 1959):

$$CS = \frac{2w}{a+b}$$

where w is the minimum sum of the frequencies of patterns in common between two genera, a is the sum of the pattern observations for one genus, and b is the sum of the pattern observations for the other genus. CS values were calculated for all pairs of the eight

colubrid genera for which a mode could be described, i.e., those with three or more pattern observations. These CS values were used to generate a similarity phenogram using Single Linkage Clustering (SLC). This method was selected because it has been widely used since the late 1950's, it is relatively simple, and it is easy to interpret (Morgan et al., 1976; Voris, 1977:90). In SLC, a matrix of all combinations of taxa and their CS values is prepared. The pair of taxa with the highest score is then lumped, and its (now combined) observations are compared with the remaining taxa in a second matrix. The procedure is repeated until all taxa have been clustered and a phenogram is generated that illustrates relative similarities among the taxa (Voris, 1969, provided a detailed example of the procedure).

C. Evaluation of Variability in the Booidea

Thirty-eight species of boids exhibited slight individual variability and no significant interspecific and intergeneric variability in coil application movements. They usually wound anterior, horizontal coils with an initial twist. This same pattern was observed in one species of acrochordid, one species of aniliid, seven species of tropidophiids, and one species of xenopeltid. Some genera (e.g., *Exilboa*) are represented by only one observation of one animal, but the low V's (Table 3) for individual characters suggest that single records for the booid pattern can adequately represent a taxon. This conclusion is further supported by high stereotypy values for 29 observations of a single *Epicrates cenchria* ($\bar{x} = .83$; range .75-.89), and by the consistently high values for 13 genera for which there were three or more observations (Table 4). Only 9 of 27 possible Scheme 2 patterns

Table 4. Stereotypy Scores for Coil Application Movements in 13 Booid Genera^a

Genera	Number of Species	Number of Individuals	Number of Observations	Stereotypy
<i>Acrantophis</i>	2	3	3	1.0
<i>Boa</i>	1	6	29	.85±.1163, .66-.93
<i>Calabaria</i>	1	1	7	.86±.0439, .79-.89
<i>Candoia</i>	2	7	9	.92±.0632, .80-.95
<i>Chondropython</i>	1	7	7	.92±.0689, .79-.96
<i>Corallus</i>	2	11	22	.96±.0469, .86-.98
<i>Epicrates</i>	7	20	161	.83±.1412, .28-.91
<i>Eryx</i>	4	5	5	.86±.0548, .80-.90
<i>Eunectes</i>	2	4	24	.88±.0839, .70-.93
<i>Liasis</i>	6	11	11	.81±.1015, .57-.89
<i>Loxocemus</i>	1	3	11	.96±.0633, .77-.98
<i>Python</i>	3	13	19	.92±.1058, .57-.97
<i>Tropidophis</i>	3	12	26	.94±.1037, .52-.97

^aBased on all characters and states. Means are followed by standard deviations and ranges.

were observed among the Booidea, and Pattern 1 was modal (or exclusive) for every species (Table 5). A_w for patterns across all observations of booids in my sample was .08, much less than the value of .46 for the entire sample of colubrids.

There is no evidence that context can influence the coil application pattern used by booids. The modal pattern was confirmed for 40 species constricting on flat or irregular substrates, 7 species striking from elevated beams, and 5 species striking in water. The prey were usually rodents, but I also observed some species constrict birds, lizards, and frogs (Table 6). A published photograph of a *Boa constrictor* constricting a coati (*Nasua narica*) in Costa Rica illustrates

Table 5. Distribution of Scheme 2 Coil Application Patterns Among 26 Genera of Primitive Snakes

Taxa	Patterns									V
	1	2	3	4	7	10	11	19	21	
Acrochordidae										
<i>Acrochordus</i>	1									0
Aniliidae										
<i>Cylindrophis</i>	2									0
Boidae										
<i>Acrantophis</i>	3									0
<i>Aspidites</i>	2									0
<i>Boa</i>	23			1	1			1		.12
<i>Bothrochilus</i>	2									0
<i>Calabaria</i>	7									0
<i>Candoia</i>	10									0
<i>Charina</i>	1									0
<i>Chondropython</i>	7									0
<i>Corallus</i>	22									0
<i>Epicrates</i>	131	2	8	2			1	5	4	.14
<i>Eryx</i>	4									0
<i>Eunectes</i>	23						1			.04
<i>Gongylophis</i>	1									0
<i>Liasis</i>	9		1							.10
<i>Lichanura</i>	1									0
<i>Loxocemus</i>	11									0
<i>Morelia</i>	1									0
<i>Python</i>	1									0
<i>Sanzinia</i>	2									0
Tropidophiidae										
<i>Exiliboa</i>	1									0
<i>Trachyboa</i>	2									0
<i>Tropidophis</i>	34		1							.03
<i>Ungaliophis</i>	1									0
Xenopeltidae										
<i>Xenopeltis</i>	2									0

V = percentage of non-modal patterns.

Table 6. Ecological and Morphological Diversity in the Booidea^a

Habitat		Diet		Adult Length	
				m	
Aquatic	≤ 5(3)	Fish	1(1)	≤ .5	5(4)
Terrestrial	36(19)	Frogs	3(3)	.6- .9	16(11)
Arboreal	7(5)	Reptiles	9(5)	1.0-1.9	15(10)
		Birds	8(6)	2.0-2.9	6(5)
		Mammals	39(22)	≥ 3.0	6(4)

^aNumber of species followed by genera in parentheses. Diet refers to kinds accepted by captives in this study.

the booid pattern in a wild snake (Janzen, 1970). Kodachromes by F. Trask show a *Python sebae* constricting an antelope in Ngorongoro Crater, Africa, and the character states that can be seen in the slides are those typically used by my laboratory snakes (these photographs are on file in the Department of Herpetology, The American Museum of Natural History)..

D. Evaluation of Variability in the Colubridae

Twenty-five species of colubrids exhibited varying amounts of individual, interspecific, and intergeneric variability in coil application movements. Each character state occurred in more than one taxon (Table 7). Variation is described below on a character by character basis.

Character I. Winding was the modal response for Character I across all observations of colubrids, as well as the modal (or only observed) state for nine genera. Wrapping was the modal state for only two genera, but was observed separately in three others and in

Table 7. Distribution of Character States for 13 Genera of Colubrids.

	I				II				III				IV						
	(1)	(2)	(3)	V	(1)	(2)	(3)	V	(1)	(2)	(3)	V	(1)	(2)	(3)	(4)	(5)	(6)	V
<i>Arizona</i>	3			0	3			0	3			0	2	1					.33
<i>Boaedon</i>	15		2	.12		17		0	17			0	6	4	1	2			.57
<i>Chrysopelas</i>	1			0		1		0	1			0					1		0
<i>Elaphe</i>	39	1	6	.15	2	44	1	.06	47			0	3	33	3		6		.36
<i>Gonyosoma</i>	5			0		3	2	.40	2	1	2	.60	1	2					.33
<i>Heterodon</i>			1	0		1		0	1			0		1					0
<i>Lampropeltis</i>	31	23	22	.59	30	28	14	.58	58	1	16	.23	19	39	13	6	4	1	.52
<i>Pituophis</i>	12		3	.20	1	13		.07	11		4	.27	3	8	1		2		.43
<i>Pseudoboa</i>	1			0		1		0	1			0	1						0
<i>Rhinocallis</i>		1	1	.50		2		0	2			0	1	1					.50
<i>Spalerosophis</i>		4		0	4			0	3	1		.25			2		1	1	.50
<i>Spilotes</i>	1	11		.08	9	2		.18	4	8		.33		7	1		1		.22
<i>Trimorphodon</i>	7		4	.36		13		0	13			0	2	6	2		1	2	.54

V = percentage of non-modal states.

combination with winding in seven. V for this character varied from 0 to .59, and $A_w = .32$.

Character II. No twist was the modal state for this character across all observations of colubrids, and the modal (or only observed) state for nine genera. Twist was the modal state for four genera, but was observed separately in two and in combination with twist in three. V for this character varied from 0 to .58, and $A_w = .28$.

Character III. Anterior was the modal state for this character across all observations of colubrids, and the modal (or only observed) state for 12 genera. Posterior was the modal state for one genus, but was observed separately in three others and in combination with anterior in three. V for this character varied from 0 to .60, and $A_w = .15$.

Character IV. Vertical was the modal state for this character across all observations of colubrids, and the modal (or only observed) state for three genera. V for this character varied from 0 to .54, and $A_w = .44$.

Stereotypy values ranged from .17 to .92 (Table 8), and there are significant differences among the scores of five genera with 10 or more observations (Table 9). The results suggest that the coil application movements of *Elaphe*, *Boaedon*, and *Trimorphodon* are relatively stereotyped, that those of *Pituophis* and *Spilotes* are somewhat less so, and that those of *Lampropeltis* are highly variable. The reason for these differences in stereotypy is not known, and further studies of the most variable taxa would be of interest.

Although 19 Scheme 2 patterns were observed among the 25 species

Table 8. Stereotypy Scores for Coil Application Movements in Nine Colubrid Genera

Genera	Number of Species	Number of Individuals	Number of Observations	Stereotypy
<i>Arizona</i>	1	2	3	.89±.0520, .83-.92
<i>Boaedon</i>	1	9	17	.78±.0734, .57-.85
<i>Elaphe</i>	10	20	47	.80±.1139, .51-.88
<i>Gonyosoma</i>	1	2	5	.59±.0685, .49-.67
<i>Lampropeltis</i>	4	11	78	.47±.1133, .23-.63
<i>Pituophis</i>	2	3	15	.65±.1706, .29-.76
<i>Spalerosophis</i>	1	2	4	.78±.1289, .63-.81
<i>Spilotes</i>	1	1	11	.64±.0602, .17-.80
<i>Trimorphodon</i>	2	5	13	.70±.0724, .61-.78

^aMeans are followed by standard deviations and ranges.

Table 9. Stereotypy Comparisons Among Six Colubrid Genera

	<i>Elaphe</i>	<i>Boaedon</i>	<i>Tri- morphodon</i>	<i>Pituophis</i>	<i>Spilotes</i>	<i>Lampro- peltis</i>
<i>Elaphe</i>	--	NS	P<.01	P<.01	P<.01	P<.01
<i>Boaedon</i>		--	P<.01	P<.01	P<.01	P<.01
<i>Trimorphodon</i>			--	NS	NS	P<.01
<i>Pituophis</i>				--	NS	P<.01
<i>Spilotes</i>					--	P<.01
<i>Lampropeltis</i>						--

Genera are listed from top to bottom in order of decreasing stereotypy, and are those for which there were 10 or more observations. Probabilities are based on Mann-Whitney U Tests.

of colubrids, one or two were consistent within most genera (Table 10). Pattern 4 (an anterior coil wound without a twist) was modal across all observations of colubrids and the modal (or only observed) pattern for eight genera. Other modal patterns were 1 (one genus), 2 (one genus), 6 (one genus), and 11 (one genus). V for the 13 genera ranged from 0 to .75, and $A_w = .46$.

A coefficient of similarity matrix (Table 11) and a SLC phenogram (Figure 8) illustrate the similarities and differences among coil application patterns in eight genera of colubrids for which there were three or more observations. Combined with variability in Character IV (Table 7), the results suggest six broad groupings of these snakes in terms of coil application movements (Table 12). The systematic implications of these groupings are discussed in the final section of this chapter.

E. Ontogeny

My observation on naive boids suggest that the descriptive characteristics of coil application in primitive snakes are present the first time they encounter prey. I observed 14 neonate *Epicrates cenchria* (from two litters), three *Corallus enydria* (from two litters), and one *Python molurus*. Although including only three species, these young snakes represent two subfamilies (Boinae, Pythoninae), three genera, and two habitat types (*Epicrates* and *Python* are terrestrial or semi-arboreal, *Corallus* is strictly arboreal). One *E. cenchria* wound an anterior coil without a twist; the other 17 neonates wound anterior coils with a twist during their first constricting attempts (Table 13), the same pattern used by adult boids.

Table 10. Distribution of Scheme 2 Coil Application Patterns Among 13 Genera of Colubrid Snakes

	1	2	3	4	5	6	7	8	11	16	19	20	21	22	23	24	25	26	27	V
<i>Arizona</i>	3																			0
<i>Boaedon</i>				10		2														.17
<i>Chrysopelea</i>				1																0
<i>Elaphe</i>	2			32		9	1													.27
<i>Gonyosoma</i>				1						1										.50
<i>Heterodon</i>						1														0
<i>Lampropeltis</i>	7	9	10	17	2	4	2	1	1		1	1	1	1	1	2	1	4	2	.75
<i>Pituophis</i>			1	10										1		2				.33
<i>Pseudoboa</i>				1																0
<i>Rhinocheilus</i>					1	1														.50
<i>Spalerosophis</i>			3						1											.25
<i>Spilotes</i>			2			1			7											.30
<i>Trimorphodon</i>				7		4														

V = percentage of non-modal patterns.

Table 11. Coefficient of Similarity Matrix for Eight Genera of Colubrid Snakes, Based on Constricting Coil Application Patterns

	A	B	E	L	P	Sa	Si	T
<i>Arizona</i> (A)	-	0	.09	.09	0	0	0	0
<i>Boaedon</i> (B)		-	.36	.30	.74	0	0	.78
<i>Elaphe</i> (E)			-	.43	.29	0	0	.40
<i>Lampropeltis</i> (L)				-	.34	.11	.10	.28
<i>Pituophis</i> (P)					-	0	0	.54
<i>Spalerosophis</i> (Sa)						-	.43	0
<i>Spilotes</i> (Si)							-	0
<i>Trimorphodon</i> (T)								-

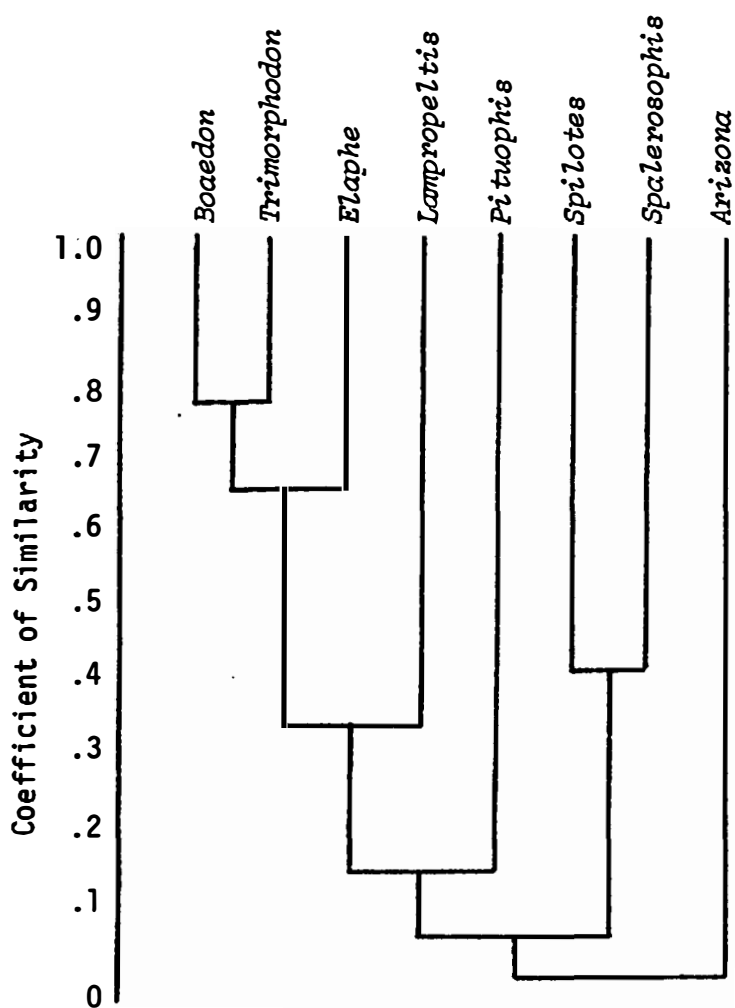


Figure 8. Single Linkage Cluster phenogram for eight genera of colubrid snakes, based on coil application behavior.

Table 12. General Characteristics of Constricting Behavior in Eight Genera of Colubrids

Genera	Coil Application Movements	Scheme 2 Patterns
<i>Arizona</i>	anterior, wound, with a twist, horizontal or vertical	1
<i>Boaedon</i>	anterior, wound (sometimes with wrapping), without a twist, horizontal or vertical	4,6
<i>Elaphe</i> , <i>Pituophis</i> , <i>Trimorphodon</i>	anterior, wound (sometimes with wrapping), without a twist, usually vertical	4,5
<i>Lampropeltis</i>	usually anterior, but highly variable in other characteristics	1-8,11, 19,27
<i>Spalerosophis</i>	anterior, wrapped, with a twist, variable coil orientation	
<i>Spilotes</i>	variable, but often posterior, wrapped, with a twist, vertical	2,5,11

Table 13. Distribution of Character States for Neonate Snakes During First Prey Encounters

Taxa	I			II			III			IV					
	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(4)	(5)	(6)
Boidae															
<i>Corallus endyris</i>	3			3			3			3			3		
<i>Epicrates cenchria</i>	14			14			14			13	1		3	1	
<i>Python molurus</i>	1			1			1			1			1		
Colubridae															
<i>Boaedon fuliginosus</i>	1		1	1	1			2					2		
<i>Chrysopelea ornata</i>	1	2		4				3	1	2				1	1
<i>Elaphe guttata</i>	2			2				2		1					
<i>E. obsoleta</i>	5	2		4	2	1	1	5	1	4		1		1	
<i>Lampropeltis getulus</i>	1		2	2	1		1	1	1	3					
<i>Pituophis melanoleucus</i>	5	1		4	2		1	4	1	1	4				1

The coil application of naive young colubrids often resembled that of adults. Cine films of one naive *Elaphe obsoleta* and one naive *E. guttata* showed that these snakes wound interior coils without a twist, as did adult rat snakes. Their coils were initially vertical but immediately fell to the horizontal. The initial winding movements were followed by wrapping with the remainder of the snakes' bodies. Checklist records of other naive neonate rat snakes (1 *E. guttata*, 6 *E. obsoleta*) demonstrate variability in the constricting behavior of newborn animals (Table 13). The modal character states were winding, anterior, no twist, and horizontal. The behavior of four juvenile *E. climacophora* during three coil application events each was more variable than adults (these young snakes initially refused to feed except in darkness, and their first prey encounters could not be observed). Stereotypy ranged from .52-.77 ($\bar{x}=.68$), and was significantly less than that of 10 observations for the two parents (.87-1.00, $\bar{x}=.98$; $P<.01$, Mann-Whitney U Test). The behavior of two neonate *Boaedon fuliginosus* and four neonate *Chrysopelea ornata* also resembled that of adults of each species, except that wrapping was used by two of the *C. ornata* (the single adult of this species that I observed wound prey). Three neonate *Lampropeltis getulus* exhibited the lack of consistency in each of three Scheme 2 characters, as did adult king-snakes. The modal response of six naive *Pituophis melanoleucus* was to wind anterior coils without twists, as did adults of this species.

These observations on neonate colubrids (Table 13) suggest that at least some aspects of coil application are innate, but that the behavior can be less stereotyped than that of adults. Experiments

are needed that carefully control for extrinsic factors (such as prey weight) during first prey encounters and for subsequent experiential effects.

F. Evaluation of Previous Studies

Pope (1961) correctly described the constricting behavior of large boids as resulting in the prey being turned about its long axis.

Frazzetta figured coil application by *Python molurus* and *P. sebae* based on film analysis, and described it as follows (1966:259):

This maneuver was performed with the forebody of the snake arched in the air and with the snout directed downward so that the blow would have the effect of forcing the prey farther back into the mouth. . . . this action appears on the films as a continuation of the strike and is executed very rapidly. . . . the prey is next brought back toward the anterior midbody or posterior forebody of the snake, a portion of which is raised so as to expose its ventral surface. . . . the prey is pressed against this exposed surface where it is enveloped by the body; the head and neck of the snake essentially roll posteriorly on the ventral body surface, each revolution producing a complete helical envirclement of the prey. Usually the prey is encircled one and one-half times and it is most often the ventral body surface that is pressed against the victim, seldom the lateral side [*sic*] as I have seen employed by constricting colubrids.

Frazzetta's account and figures confirm my description of the movements used by boids to apply coils.

Shrewsbury (1969) observed constricting behavior by six *Lampropeltis getulus*, one *L. calligaster*, four *Elaphe obsoleta*, one *E. guttata*, and one *E. vulpina*. He reported that all snakes wound prey in vertical coils, although the coils sometimes fell over. His *Lampropeltis* constricted with venters forward (with a twist) and his *Elpae* with venters backward (no twist). He stated that the *Lampropeltis* usually fell over and suggested that this was because, owing to the initial twist, they

would be resting on their backs if they remained vertical. Shrewsbury noted that some of the snakes formed "balls of total confusion," and that this seemed to reflect a capacity for making continuous adjustments to prey movements. My survey shows that Shrewsbury's observations were accurate, although not sufficiently detailed to describe the patterns and variation in a larger sample of species.

Franz (1977) reported that a *Regina alleni* "threw" two and one-half coils around a crayfish, then released the prey with its jaws and moved to the posterior end to ingest it. His drawing indicates that most or all of the snake was involved in the coil, that an initial twist was present (the snake's venter is against the prey), and that perhaps the prey was wound (the crayfish has its venter facing up). If the drawing accurately illustrates these points, the *R. alleni* used a coil application pattern that is quite rare among colubrids and present in primitive snakes.

Murphy (1977) described coil application by three specimens of a large, rear-fanged colubrid, *Boiga cynodon*. These snakes seized chicks and applied loops by "snaking" the tail around the prey to form (judging from his figure) an irregular coil using both ventral and lateral surfaces. Murphy cited unpublished observations by J. A. Campbell that *B. dendrophila* used similar movements to apply coils, and Wall's (1970:549) observations suggest that this is also the case for *B. trigonata*. This pattern of coil application might be typical of those species of *Boiga* that constrict, but the conclusion that it is unique to these snakes (Murphy, 1977) is not yet warranted. I observed individual *Spilotes pullatus* and *Lampropeltis pyromelana* occasionally apply loops in a very similar manner.

Willard (1977) reported on 1472 observations of constricting behavior by 500 snakes, including 22 species of boids (12 genera) and 19 species (8 genera) of colubrids (Willard claimed to have studied 95 species; his Table 1 lists 43 species, and 2 of these [*Corallus hortulanus* (= *enydris*), *Pituophis catenifer* (= *melanoleucus*)] are considered conspecific with others he studied). His survey was unduly restricted by an assumption:

Geometry limits to four the ways a snake can coil around its prey: venter toward the prey, dorsum toward the prey, left lateral side [sic] toward the prey and right lateral side toward the prey. However, snake's anatomies further limit the ways with which constriction can be effective. No snake can make a circle of sufficiently small diameter to apply pressure to a prey by coiling, dorsally, and the minimum size of the circle achieved by ventral coiling is also prohibitively large, although it is sometimes used on the first coil among some boids. By using only the lateral surfaces snakes may wrap themselves either with the dorsum toward the head . . . or venter toward the head. . . (Willard, 1977:381).

Willard thus recognized only three "methods" of coil application: (1) those with venter facing forwards, (2) those with venter facing backward, and (3) irregular coils with no consistent surface against the prey. Two of these methods are equivalent to two states of one character that I used (twist [1] and no twist [2]), and the third is so ill-defined as to be of limited value for comparative studies. The methods therefore do not adequately characterize the behavior of particular species or of variation among taxa, because they omit certain useful variables. Willard (1977) was unaware of Shrewsbury's (1969) paper and, although he mentioned that coil application could involve twisting of the prey by the snake, he did not use this variable (wrapping versus winding) to describe interspecific patterns. Although differences in coil composition are implied in his descriptions of

the three methods, this character and long axis orientation were not explicitly used to characterize variability.

Willard's (1977) sample included 20 species of boids that I studied, as well as *Corallus annulatus* and *Python sebae*. He reported that all 22 species of boids used method 1, which is consistent with my finding that boids normally have a twist in the first loop. His figure of a *Corallus annulatus* accurately depicts an anterior, horizontal coil with a twist in the first loop, and the position of the rodent suggests that it was wound. Willard observed seven species of *Elaphe* (including three I studied, as well as *vulpina*, *diadema quatuorlineata*, and *quadrivirgata*), *Coronella austriaca* (which I did not study), *Farcacia abacura* and *F. erythrogramma* (which I did not study), four species of *Lampropeltis* (three that I studied and *zonata*), and *Clelia clelia* (which I did not study). He reported that these snakes always used method 2. This is consistent with my observations that *Elaphe* normally does not have a twist in the first loop. His Fig. 2 accurately indicates an *Elaphe obsoleta* constricting with an anterior coil without a twist in the first loop. However, the figure suggests a horizontal coil, whereas Shrewsbury (1969) and I usually observed vertical coils in *Elaphe*. Willard reported that *Pituophis* usually used method 2 (agreeing with my finding of no initial twist), and sometimes method 3. He reported that *Cemophora coccinea* and *Rhinocheilus lecontei* used method 3, but it is difficult to draw any conclusions about this. Willard (1977) observed that *Arizona elegans* usually used method 1 (occasionally method 3) and noted that it thus resembled the coils of boids, a finding that agrees with mine.

Greenwald (ms) reported the only study of constricting coil application movements in a colubrid using high speed cinematography. She analyzed the movements of *Pituophis* by cine film analysis ($\bar{x}$ = 85 fps), and described two methods of encirclement: in one, the snake seized the prey about its long axis in a vertical coil; this was observed in 20 of 33 sequences and by at least 5 of 6 snakes studied. In the second method a loop of the body was placed around the prey, in addition to the initial lateral flexure (a prelude to winding) of the neck and head. This was observed in nine sequences and by 5 of the 6 snakes. In four sequences the prey was not encircled, but rather pressed against an adjacent surface or smothered in the mouth. Thus, her description of the modal response in *Pituophis* is of an anterior, wound, vertical coil without a twist (Scheme 2, Pattern 4). Greenwald's observations, based on more sophisticated methods of analysis, confirm my characterization of constriction in *Pituophis*.

G. Systematic Relationships and Coil Application in the Booidea

Unlike colubrids, constricting behavior in primitive snakes is consistently similar across the five families that I studied. The significance of this similarity can now be assessed using the approach described in Chapter 2.

The diversity of prey types and substrates that I used and the presence of the adult mode in newborn snakes refute individual experience as an exclusive explanation of similar coil application among all booids. Convergence is also unlikely, because my sample included 19 of the 20 genera of boids (only the monotypic *Xenoboa* was not studied) and the

four genera of tropidophiids. These taxa encompassed most of the substantial ecological and morphological variation in these families (Table 7, page 52). For example, I observed *Exiliboa placata*, a 30 cm terrestrial cloud forest tropidophiid that eats amphibians; *Eryx johnii*, a 75 cm fossorial desert boa that eats lizards and rodents; *Corallus caninus*, a 1.5 m tree boa that eats birds; and *Eunectes murinus*, the semiaquatic anaconda, that reaches a length of over 8 m and feeds on a variety of vertebrates. Although most boids are relatively stout-bodied, my sample included the extremely slender Hispaniolan vine boa, *Epicrates gracilis*.

Since chance, individual experience, and convergence are highly unlikely explanations for the coil application behavior of extant boids, I conclude that the similarity reflects the shared retention of an action pattern used by their common ancestor. The broader implications of this conclusion are discussed in Chapter 6.

H. Systematic Relationships and Coil Application in the Colubridae

Any conclusions regarding coil application patterns in colubrids must be considered extremely tentative for three reasons: (i) Our knowledge of intergeneric relationships is very poor, recent efforts notwithstanding (e.g., Underwood, 1967). (ii) The coil application patterns of only a few genera have been studied. Moreover, in some of those that have been observed the variability has not been adequately characterized (e.g., *Heterodon*, *Rhinocheilus*); in others the *basis* for the variability is not known (e.g., *Lampropeltis*). (iii) I see no

basis at this point for determining polarity among the observed patterns, if indeed they even represent a primitive-derived series. Steward (1971) suggested (based apparently on observations of several European colubrids) that constriction arose from a tendency to turn struggling prey laterally against the anterior trunk region. This act is in fact part of the initial winding movement in some genera (e.g., *Elaphe*). It is possible that each of the patterns observed thus far in colubrids arose *de novo* from some such precursor behavior. With these reservations, I offer the following comments on colubrid constricting behavior and phylogeny for their heuristic value.

It is clear that a single pattern (or pair of related patterns, such as 4 and 6 in Scheme 2) is consistently modal within several genera, suggesting that it might be homologous within these taxa. The New World genera *Pituophis* and *Elaphe* resemble each other in coil application behavior. These genera are usually regarded as closely related (Minton and Salanitra, 1972), and there is even some doubt that they are distinct (D. J. Morafka, pers. comm.). The coil application behavior of these snakes is consistent with their supposed close relationship. *Boaedon* (African) and *Trimorphodon* (southwestern United States and Middle America) also exhibit this same pattern, and the latter genus shows some resemblance to *Elaphe* in serum proteins (Minton and Salanitra, 1972). McDowell (1975) has suggested on anatomical grounds that *Boaedon* is one of the most primitive living colubrid genera; the similarity of its constricting behavior to the New World genera could either represent convergence or the shared retention of a primitive (within the Colubridae) action pattern.

Lampropeltis has been mentioned as a specialized offshoot of *Elaphe* (Minton and Salanito, 1972), but it differs from *Elaphe* in exhibiting great variability in coil application. This variability might represent either a derivation from the *Elaphe* pattern (if *Elaphe* is instead derived from a *Lampropeltis*-like ancestor, which I suggest is equally likely at present), or an independently evolved condition. An anomaly in the SLC phenogram (Figure 8, page 58) bears comment here. When the cluster *Boaedon-Elaphe-Trimorphodon* was compared with other taxa in the third matrix of the procedure, *Lampropeltis* and *Pituophis* had similarity coefficients of .36 and .34, respectively. It is possible that a larger sample of *Pituophis* would have clustered with *Boaedon-Elaphe-Trimorphodon* before *Lampropeltis*, and for this reason I have reservations about the linkages among these snakes.

Arizona is sometimes considered a relative of *Elaphe* and *Pituophis* (e.g., Oldak, 1976). However, *Arizona* has a coil application pattern that is quite distinct from the latter genera (Table 12, page 59; Figure 8), but one that occurs occasionally in *Lampropeltis*. It might also be relevant that *Arizona* resembles *Lampropeltis* in food habits (reptiles are important in their diets) more than it resembles *Elaphe* and *Pituophis* (which, at least as adults, feed largely on rodents; Wright and Wright, 1957). The ethological and ecological data suggest that a reevaluation of relationships among these snakes is called for.

The data do not warrant speculation on *Chrysopelea*, *Gonyosoma*, *Heterodon*, *Rhinocheilus*, *Spalerosophis*, or *Spilotes*. It is sufficient to point out that constricting coil application patterns might prove useful in evaluating intergeneric relationships among colubrids. Further studies of more individuals and more taxa are clearly called for.

CHAPTER 5

DEFENSIVE DISPLAYS

A. Introduction

Snakes exhibit a variety of antipredator responses, including the following: displaying the tail, flattening all or part of the body, gaping, erratic thrashing of the body, sound production, offensive chemical discharge, biting, inflating all or part of the body, elevating the head, death feigning, immobility, forming elevated "bridges" with the body, compressing the anterior part of the body laterally, and spreading the posterior part of the head at the quadratomandibular articulations. Snake defensive behavior has not been reviewed since Mertens (1946), and most of the subsequent literature consists of anecdotal accounts for one or a few species.

The available information on the ontogeny of these responses suggests that they are innate. There are published photographs of cobras (*Naja*, Tryon, 1976; *Ophiophagus*, Oliver, 1956) rearing with spread hoods as they emerged from eggs. Species typical defensive postures and movements have also been observed in neonates of *Dispholidus typus* (Zingg, 1968), *Heterodon platyrhinos* (Rann, 1962; Kennedy, 1961; Burghardt et al., in preparation), *Ninia sebae* (Greene, 1975), and *Pituophis melanoleucus* (Greene, unpublished).

Most kinds of defensive responses in snakes are either extremely widespread or restricted to a few species with very similar ecological correlates. They are thus not appropriate for the comparative

approach suggested in Chapter 2. For example, cloacal discharge and biting occur in many species (Mertens, 1946) and apparently are not associated with any broad set of selective factors. Sound production by specialized scales is found only in two genera of Old World desert vipers (*Cerastes*, *Echis*) and the egg-eating snakes (*Dasypeltis*) that mimic them (Gans and Maderson, 1973). Here I summarize the literature and my observations on snakes that are known to exhibit either tail displays, vertical head displays, or horizontal head displays (Table 14). These modal action patterns have demonstrable ecological correlates, and it is possible to show that they have probably been convergently acquired in a number of unrelated taxa.

B. Methods

A tail display is defined as a postural shift in which the tail is made more prominent than it is in a non-predator context (Greene, 1973b:155). The exact topography of the movements varies, and can consist of (i) simply elevating the tail, and in some cases moving it back and forth (e.g., *Cylindrophis*, *Charina*, *Eryx*, *Elapsoidea*, *Atractaspis*); (ii) elevating the tail in a tightly coiled spiral with either the ventral (e.g., *Diadophis*, *Farcancia*, *Pseudechis*) or dorsal (e.g., *Epicrates*) surface uppermost; (iii) elevating the tightly coiled tail and waving it back and forth (e.g., *Micrurus*).

A vertical head display is defined as a movements and its resultant posture (or a suite of such changes) that increase the dorsoventral dimensions of the anterior part of the snake's body. This always includes either flattening the anterior portion laterally or inflating it. It often also includes gaping, spreading the posterior part of the

Table 14. Defensive Displays in 124 Species of Snakes

Taxa	Habitat	Display	References
Aniliidae			
<i>Anilius scytale</i>	T	TD	Greene (1973b)
<i>Cylindrophis</i> (4 species)	T	TD	Greene (1973b)
Boidae			
<i>Aspidites melanocephalus</i>	T	VD	Johnson (1975)
<i>Calabaria reinhardtii</i>	T	TD	Greene (1973b)
<i>Charina bottae</i>	T	TD	Greene (1973b)
<i>Epicrates cenchria</i>	T	TD	Greene (1973b)
<i>Eryx</i> (4 species)	T	TD	Greene (1973b)
<i>Python sebae</i>	T	TD	Greene (1973b)
Tropidophiidae			
<i>Ahaetulla boiga</i>	A	VD	Mertens (1930)
<i>Alsophis angulifer</i>	T	HD	Barbour & Ramsden (1919)
<i>Apostolepis ambinigra</i>	T	TD	Greene (1973b)
<i>Argroena fasciolatus</i>	T	HD	Wilson (1967)
<i>Atractaspis</i> (2 species)	T	TD	Greene (1977)
<i>Attractus elaps</i> (=poeppig.)	T	TD	Greene (1973b)
<i>Boiga dendrophila</i>	A	VD	Greene (unpubl.)
<i>Calamaria septentrionalis</i>	T	TD	Greene (1973b)
<i>Cemophora coccinea</i>	T	TD	Greene (1973b)
<i>Chilorchinophis</i> (3 species)	T	TD	Greene (1973b)
<i>Chilomeniscus cinctus</i>	T	TD	Greene (1973b)
<i>Chionactis occipitalis</i>	T	TD	Greene (1973b)
<i>Chironius carinatus</i>	A	VD	Mole (1924), Test et al. (1966)
<i>Coniophanes imperialis</i>	T	TD	Greene (1973b)
<i>Crotaphopeltis hotamboeia</i>	T	HD	Broadley (1959)
<i>Dendrelaphis punctularius</i>	A	VD	Johnson (1975)
<i>Dendrophidion percarinatum</i>	T	HD	Test et al. (1966)
<i>Diadophis punctatus</i>	T	TD	Greene (1973b)
<i>Dispholidus typus</i>	A	VD	FitzSimons (1962)
<i>Drymarchon corais</i>	T	VD,TD	Mole (1924), Greene (1973b)
<i>Dryophis</i> (2 species)	A	VD	Wall (1906a), Mertens (1930)
<i>Elaphe radiata</i>	T		
<i>Elapomorphus bilineatus</i>	T	TD	Greene (1973b)
<i>Erythrolamprus</i> (2 species)	T	TD,HD	Greene (1973b and unpubl.)
<i>Farancia</i> (2 species)	T	TD	Greene (1973b)
<i>Gonyosoma oxycephalum</i>	A	VD	Greene (unpubl.)
<i>Heterodon</i> (3 species)	T	TD,HD	Greene (1973b), Platt (1969)
<i>Hypsiglena ochrorhyncha</i>	T	HD	Webb (1970)
<i>Lampropeltis triangulum</i>	T	TD	Greene (1973b), Platt (1969)
<i>Leimadophis</i> (4 species)	T	HD	Mole (1924), Taylor (1951), Test et al. (1966)
<i>Liophis anomalus</i>	T	TD	Greene (1973b)
<i>Lystrophis dorbignyi</i>	T	TD	Greene (1973b)
<i>Lytorhynchus</i> (2 species)	T	TD	Greene (1973b)
<i>Macropisthodon rhodomelas</i>	T	HD	Taylor (1965)

Table 14 (continued)

Taxa	Habitat	Display	References
<i>Malpolon moilensis</i>	T	HD	Mandaville (1967)
<i>Ninia sebae</i>	T	HD	Greene (1975)
<i>Oligodon</i> (5 species)	T	TD	Greene (1973b)
<i>O. arnensis</i>	T	HD	Wall (1907)
<i>Philothamnus</i> (2 species)	A	VD	FitzSimons (1962)
<i>Phyllorhynchus decuratus</i>	T	VD	Greene (1973b)
<i>Pliocercus elapoides</i>	T	TD	Greene (1973b)
<i>Pseustes</i> (2 species)	A	VD	Mole (1924), Netting (1936), Rand and Ortleb (1969), Rossman and Williams (1966)
<i>Ptyas mucosas</i>	T	VD	Wall (1906b)
<i>Rhabdophis subminiatus</i>	T	HD	Taylor (1965)
<i>Rhinocheilus lecontei</i>	T	TD	Greene (1973b)
<i>Spilotes pullatus</i>	A	VD	Mole (1924), Amaral (1929), Rossman & Williams (1966)
<i>Thamnophis eques</i>	T	TD	Greene (1973b)
<i>Thelotornis kirtlandi</i>	A	VD	FitzSimons (1962)
<i>Toluca lineata</i>	T	HD	H. M. Smith (1943)
<i>Xenodon newiedii</i>	T	HD	Müller (1971)
Elapidae			
<i>Aspidelaps</i> (2 species)	T	HD	Mertens (1955)
<i>Bungarus</i> (2 species)	T	TD	Greene (1973b)
<i>Calliophis melanurus</i>	T	TD	Greene (1973b)
<i>Dendroaspis polylepis</i>	T	HD	FitzSimons (1962)
<i>Elapsoidea</i> (2 species)	T	TD	Greene (1973b)
<i>Hemachatus haemachatus</i>	T	HD	FitzSimons (1962)
<i>Leptomicrurus</i> sp.	T	TD	Greene (1973b)
<i>Maticora</i> (2 species)	T	TD	Greene (1973b)
<i>Micruroides euryxanthus</i>	T	TD	Greene (1973b)
<i>Micrurus</i> (16 species)	T	TD	Greene (1973b)
<i>Naja</i> (6 species)	T	HD	FitzSimons (1962), M. A. Smith (1943)
<i>Notechis scutatus</i>	T	HD	Johnson (1975)
<i>Ophiophagus hannah</i>	T	HD	M. A. Smith (1943)
<i>Pseudechis porphyriacus</i>	T	TD	Greene (1973b)
<i>Rhinelaps warro</i>	T	TD	Johnson (1975)
<i>Vermicella annulata</i>	T	TD	Johnson (1975)
Viperidae			
<i>Causus rhombeatus</i>	T	HD	M. A. Smith (1943)
<i>Trimeresurus gramineus</i>	A	TD	Greene (1973b)

head, and drawing the body back into an exaggerated S-shaped coil.

Information on vertical head displays was obtained from the literature and from field and laboratory observation.

A horizontal head display is defined as a movement and its resultant posture that increases the lateral dimensions of the anterior part of the snake's body. It always involves flattening the anterior portion dorsoventrally, presumably by moving the ribs forward. Horizontal head displays are often accompanied by gaping and by elevating the head and anterior part of the body.

I have records of 124 species in 76 genera and 6 families that exhibit either tail displays, vertical head displays, horizontal head displays, or a combination of two of these. Each species was classed as either (i) fossorial and/or terrestrial but not arboreal or (ii) arboreal or arboreal and terrestrial. A 2 x 3 comparison of 73 genera according to habitat and defensive behavior was tested for independence with a Chi Square test. I did not use individual species for this analysis, because all species in most genera used the same kind of display and because the 16 species of *Micromys* would have excessively inflated the comparison. Three genera (*Drymarchon*, *Erythrolamprus*, *Oligodon*) were recorded to use two types of displays and were excluded because of the requirements of the statistical test.

C. Results and Discussion

The results demonstrate that defensive display types are significantly associated with habitat types (Table 15, $P < .01$). Tail displays are almost entirely restricted to terrestrial or fossorial

Table 15. Relationship of Habitat to Defensive Display Behavior

Habitat	TD	VD	HD
Fossorial or Terrestrial	38	3	19
Arboreal	1	12	0

Abbreviations are for tail display (TD), vertical head display (VD), and horizontal head display (HD).

snakes (97.6% of 42 genera with this behavior). These snakes are assigned to six families, and four of them (Boidae, Colubridae, Elapidae, Viperidae) include arboreal species that do not have tail displays. It thus appears likely that the similarities among the defensive behaviors are due to convergence. This conclusion is strengthened by a further consideration of three genera. African mole vipers (*Atractaspis*) are small (less than 1 m total length), burrowing snakes that feed on lizards, snakes, and small mammals. Their defensive behavior includes hiding the head, flattening and erratically snapping the body, elevating and curling the tail, and biting (Greene, 1977). Venomous New World coral snakes (*Leptomicrurus*, *Micruroides*, *Micrurus*) are small (usually less than 1 m total length), inhabit forest litter, and feed on small snakes and other elongate vertebrates (Greene, 1973a). Their defensive behavior is virtually identical with that of *Atractaspis*, except that the somewhat longer tail of *Micrurus* is usually coiled in a loop when it is elevated. False coral snakes (*Erythrolamprus* sp.) are similar in size, coloration, and ecology to *Micrurus*. They have very similar defensive behavior, except that the anterior portion of the body is sometimes flattened and elevated

in *Erythrolamprus* (Greene, unpublished). In short, *Atractaspis*, *Erythrolamprus*, and *Micrurus* are unrelated, are more or less ecological equivalents, and have very similar defensive displays. The behavioral and color pattern resemblances of *Erythrolamprus* and *Micrurus* may be a case of Müllerian mimicry (Greene and Pyburn, 1973).

Vertical head displays predominate in arboreal snakes (75% of 16 arboreal genera), and are much less common among the terrestrial species (8.9% of the 45 terrestrial or fossorial genera in the comparison). The arboreal colubrids include nine Old World (*Ahaetulla*, *Boiga*, *Dendrelaphis*, *Dispholidus*, *Dryophis*, *Elaphe*, *Gonyosoma*, *Philothamnus*, *Thelotornis*) and three New World (*Chironius*, *Pseustes*, *Spilotes*) genera. With two exceptions (*Pseustes* and *Spilotes*, *Dispholidus* and *Thelotornis*), I know of no evidence to indicate close relationships among them; they would be placed in at least four subfamilies in Smith et al.'s (1977) classification of colubrids. It is therefore likely that the similarities in defensive displays among these genera, at least in most instances, is due to convergence and not homology.

A more refined comparison between two species underscores the conclusion that vertical head displays are convergent among arboreal snakes. *Pseustes poecilonotus* is a large (ca. 2 m total length), diurnal, arboreal, Neotropical rain forest snake that feeds largely on birds. Rand and Ortleb (1969) described the defensive behavior of this species, and my field observations on three specimens in Panama agree with theirs. The defensive display of *P. poecilonotus* includes lateral compression of the body, spreading of the lower jaws at the quadrato-mandibular joints, inflating the anterior trunk, opening the mouth, and

striking. The overall effect to a human observer is to greatly increase the apparent size of the anterior part of the snake, and perhaps (Rand and Ortleb, 1969) to increase resemblance to a venomous pit viper.

The mangrove snake, *Boiga dendrophila*, of southeastern Asia and the Philippines is an ecological equivalent of *P. poecilonotus*. It is large, nocturnal, arboreal, and feeds on birds in tropical rain forests. Three *B. dendrophila* that I observed in the Knoxville Zoological Park exhibited defensive behavior that was very similar to that of *Pseustes*, not only in the component postures but also the approximate order of their appearance in the display. I know of no evidence that these two species are more closely related to each other than to any other snakes in the world, and they would be placed in different subfamilies in Smith et al.'s (1977) scheme of colubrid classification.

Horizontal head displays are restricted to terrestrial species in my sample, including 13 Old World genera (*Argyrogena*, *Crotaphopeltis*, *Macropisthodon*, *Malpolon*, *Oligodon*, *Rhabdophis*, *Aspidelaps*, *Dendroaspis*, *Hemachatus*, *Naja*, *Notechis*, *Ophiophagus*, *Causus*) and nine New World genera (*Alsophis*, *Dendrophidion*, *Erythrolamprus*, *Heterodon*, *Hypsigena*, *Leimadophis*, *Ninia*, *Toluca*, *Xenodon*). These snakes represent three families, and the colubrids would be placed in at least five subfamilies in Smith et al.'s (1977) classification. Given the taxonomic and geographic diversity represented by the 22 genera, much of the similarity in defensive behavior among these snakes is probably due to convergence.

More sophisticated studies of these and other snakes will permit further evaluation of the origins of similarities among their defensive displays. This preliminary consideration demonstrates that the number

of possible antipredator responses available to snakes is quite limited, and that convergence has probably been widespread.

CHAPTER 6

EPILOGUE

Behavioral information . . . can make a more significant contribution to the analysis of evolution by providing concrete, immediate, information to help explain certain ecological phenomena, developments, and interactions which are themselves among the causes of evolutionary changes (Moynihan, 1973:22).

O body swayed to music, O brightening glance,
How can we know the dancer from the dance?
(William Butler Yeats, *Among School Children*)

A. Introduction

Comparative studies of behavior can have at least five important applications to evolutionary biology: (i) They can elucidate the mechanisms of interactions among different species, such as reproductive isolation and the promotion of sympatry via ecological niche differences (Klopfer, 1973c). (ii) They can be used in connection with other characters to determine the relationships among taxa (e.g., Carpenter, 1962). (iii) When homologies can be established and a fossil record is available of separate lineages in a group, they can provide an estimate of the minimum age of a behavior (Moynihan, 1973 [see pp. 2-18]; Fig. 9). (iv) The behavior can then be correlated with morphology and paleoecology to suggest selective factors in the adaptive radiation of the group. (v) They can point to particular adaptive functions when convergence is demonstrated (e.g., Eisenberg et al., 1972; Barash, 1974; Dewsbury, 1975). Goals (i), (ii), and (v) have been widely realized in the literature, but (iii) and (iv), perhaps alluded to in Moynihan's quote above, are generally unappreciated

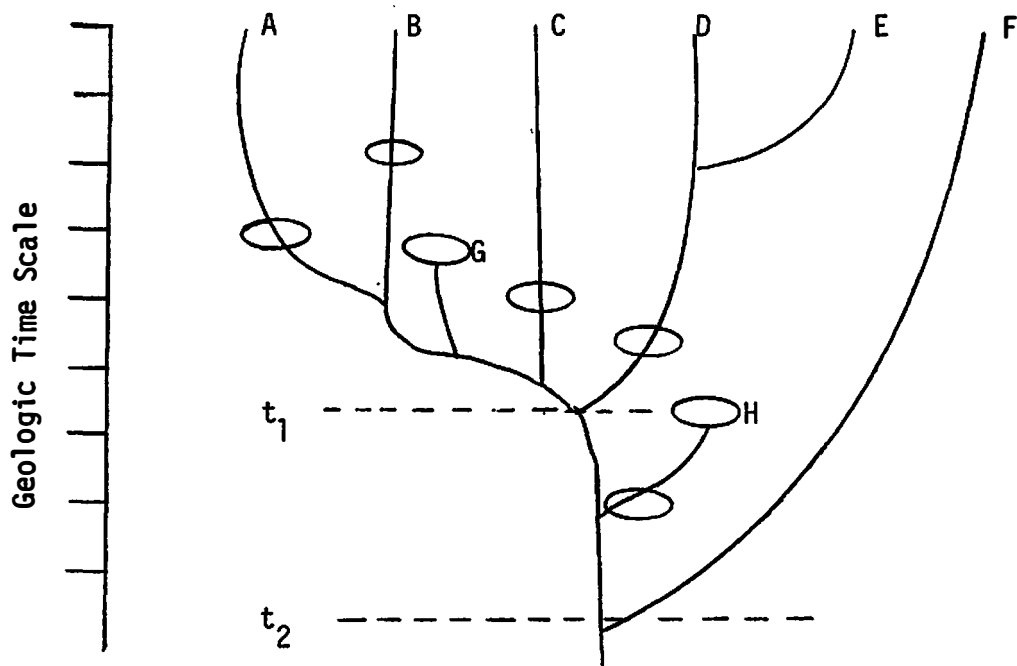


Figure 9. Behavioral homologies and the minimum age of a behavior pattern. Taxa A through F are related living species of diverse morphologies and ecologies that are found to exhibit similar behaviors. Ovals represent the known fossils of these taxa as distinct evolutionary lineages. Line t_1 represents the most recent time at which the homologous behavior could have appeared in a common ancestor on the basis of studies of A through E. At this point, nothing can be said about the behavior of extinct form H, but extinct form G probably exhibited the behavior unless it was secondarily lost. If subsequent studies show modern taxon F to exhibit the homologous behavior, its minimum age can be re-estimated as t_2 . With this new information, the remarks concerning taxon G also apply to H.

by contemporary ethologists. My studies of snake behavior are relevant to goals (ii) through (v).

B. Implications of Constricting Behavior in the Booidea

Minton and Minton (1973:217-218) suggested that constriction must have appeared early in the evolution of snakes because of its "high development in primitive boas and pythons." They also speculated on the origin of constriction:

Perhaps it developed from the crocodilian and lizard trait of grasping large prey in the jaws and twisting or whirling with it in order to dismember it. If a proto-snake tried this, it would tend to twist its own body around that of the victim, and muscles ordinarily used for locomotion would now apply pressure.

Three lines of evidence suggests that the constricting application pattern of modern boids is indeed an extremely ancient behavior. (i) Fossils of the boid subfamilies Boinae, Erycinae, and Pythoninae indicate some divergence at least as early as the Paleocene (Underwood, 1976; Figure 10) and Underwood argued that the initial radiation of these snakes began in the Cretaceous. My sample included these taxa, as well as the even more primitive Loxoceminae (which lacks a fossil record) and the Tropicophiidae (a relict from the Cretaceous, according to Underwood, 1976). If the coil application patterns of Recent boids and tropidophiids are homologous, the ancestors of these snakes constricted prey in the Paleocene, and perhaps much earlier in the Cretaceous. (ii) *Acrochordus javanicus*, *Cylindrophis rufus*, and *Xenopeltis unicolor* are usually considered survivors of proboid stock (Underwood, 1976; McDowell, in press a). If my observations of these species accurately indicate their constricting behavior, this pattern of coil application might date back

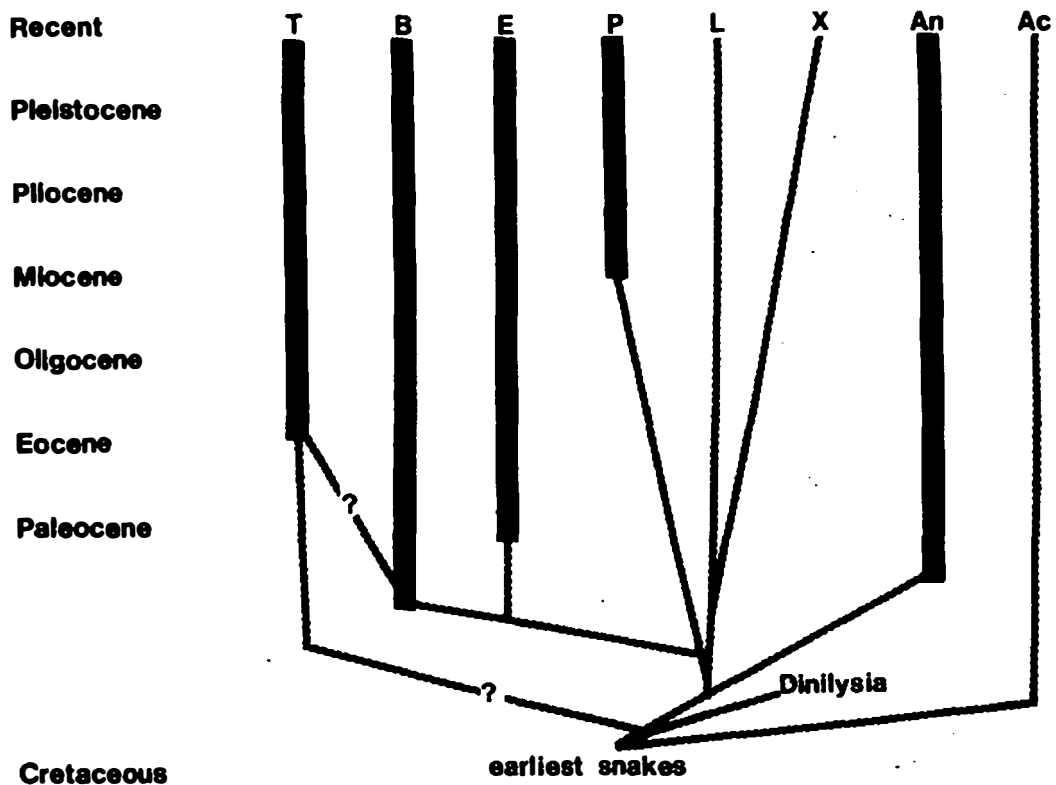


Figure 10. Evolutionary history of primitive constricting snakes.

Dark bars indicate known fossil histories; wavy lines indicate presumed relationships based on comparative morphology. Abbreviations indicate the taxa Tropidophiidae (T), Boinae (B), Erycinae (E), Pythoninae (P), Loxoceminae (L), Xenopeltidae (X), Aniliidae (An), and Acrochordidae (Ac). *Dinilysia* is the oldest well-known fossil snake.

to the earliest snakes. (iii) Some aspects of the feeding behavior of anguimorph lizards resemble that of coil application in primitive snakes. Assuming that the Anguimorpha is the sister group of early snakes (Chapter 3), the behavior of these animals can be used for an "out group comparison" (Hecht, 1976; see also Chapter 2). I observed lizards of the families Anguidae, Varanidae, Helodermatidae, and Xenosauridae to pin struggling prey to the substrate with a forward, downward, and lateral twist of the neck and head, so that the neck was lifted and turned to one side or the other. This maneuver seemed to immobilize prey, and in some cases it was crushed against the substrate. In one instance a Gila monster, *Heloderma suspectum*, continued this twisting movement and spun one revolution about its long axis. The prey (a mouse) was simultaneously turned, and if the lizard had been long and slender (rather than very stout-bodied) it would have wound an anterior, horizontal coil with an initial twist. These observations support the conclusion that the coil application pattern of booid snakes is a shared primitive feature that was present in their common ancestor. As such, it can not be used in systematic studies to separate those snakes that exhibit the behavior from those that do not (see pp. 20-21).

Functional innovations are often thought to provide a "proto-adaptive" advantage for subsequent structural changes during the origin of new adaptive radiations (Gans, 1969, 1974), but there is rarely evidence for the presence or timing of such shifts. As ancestral snakes evolved increased gape there would have been an advantage to tactics for overpowering large prey too strong to have been eaten while it struggled (Gans, 1961). It follows that constriction might have been a behavioral protoadaptation that permitted the evolutionary loss of the

mandibular symphysis and development of a highly movable (streptostylic) quadrate bone, the key modifications for ingesting large items (Gans, 1961; Kardong, 1977). However, Frazzetta (1970) suggested that *Dinilysia patagonica*, the earliest well-known snake, was not a constrictor. Like aniliids (its apparent closest living relatives, *fide* Estes, Frazzetta, and Williams, 1970), the stout jaws of *D. patagonica* seem well-suited for crushing prey, and the aniliids that Frazzetta observed (species not stated) did not constrict. Furthermore, birds and mammals, thought to be especially vulnerable to constriction because of high metabolic rates, were not yet widespread in the Cretaceous. These arguments are weakened by the fact that many Recent booid snakes use constriction to subdue ectotherms: I have observed constriction of snakes by *Cylindrophis rufus* (Aniliidae); of lizards by one species of *Ungaliophis* and three species of *Tropidophis* (Tropidophiidae), two species of *Epicrates* (Boidae), and *Loxocemus bicolor* (Boidae); and of frogs by one species each of *Tropidophis*, *Exiliboa*, and *Trachyboa* (Tropidophiidae). More importantly, my study demonstrates the great antiquity of constriction in boids and probably the entire superfamily Booidea. I therefore suggest that *D. patagonica* more likely did constrict prey, and that this behavior was an ethological "key innovation" (Liem, 1973) in the early evolution of snakes.

C. Implications of Constricting Behavior in the Colubridae

The application of constricting behavior patterns to questions of colubrid evolution must await further studies of variability within

and between taxa. The consistency within some genera suggests that coil application movements might be homologous, and a broader survey of constricting behavior (coupled with more information on relationships from other sources) might eventually permit a sound evaluation of similarities and differences. Comparisons with the fossil record could then provide some insight into the explosive mid-Tertiary radiation of these animals, and their subsequent domination of the world snake fauna. It is suggestive that some modern genera date back to the Miocene, and that their appearance coincides (at least roughly) with the appearance of rodents in the fossil record (Rabb and Marx, 1973). An obvious hypothesis is that the origins of these genera (e.g., *Elaphe*) began when a behavioral shift to constricting made possible the exploitation of a new and perhaps abundant food resource.

D. Implications of Defensive Behavior

The survey of antipredator behavior patterns implies that snakes are limited by morphological constraints to a few possible defensive displays, and that the forms of displays are rather tightly coupled to immediate selective pressures: the predation problems faced by the snake populations at a particular time and place. This suggests in turn that defensive adaptations of snakes are superimposed at the population, species, or at most the generic broad adaptive zones. For example, all boids constrict prey but defensive tail displays are largely restricted to small or medium length burrowing species (*Calabaria*, *Charina*, *Eryx*). Possible reciprocal interactions among feeding, defense, and morphological adaptations remain to be studied.

E. Conclusion

Mayr (1969:137), in a discussion of behavioral characters in taxonomy, remarked that similar patterns are very rarely encountered among higher taxa. A subsequent review concluded that there are no compelling cases of behavioral homologies above the family level in vertebrates (Atz, 1970). My studies show that a single modal action pattern used in feeding is probably homologous among at least four families of primitive snakes. Other patterns are perhaps homologous within each of several genera of advanced snakes. The preliminary survey of defensive displays demonstrates that similarities in another kind of behavior often reflect convergence in response to common ecological pressures, rather than common ancestry. Taken together, these results point to broader issues: What kinds of motor patterns are stable over long periods of evolutionary time? What kinds change rapidly, and why? How are the rates and directions of change constrained by other factors? Rigorous comparative studies might provide answers to these and other questions regarding the evolution of behavior and the role of behavior in evolution.

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APPENDICES

APPENDIX A

ADDITIONAL SNAKES KNOWN TO CONSTRICT PREY

Aniliidae

Cylindrophis maculatus (C. Gans, in litt.).

Boidae

Corallus annulatus (Willard, 1977), *Python curtus* (Willard, 1977), *P. reticulatus* (Willard, 1977).

Tropidophiidae

Tropidophis caymanensis (Edwards, 1969), *T. Maculatus* (Petzold, 1969), *T. melaniurus* Petzold, 1969).

Colubridae

Alsophis cantherigerus (Petzold, 1969), *Boiga cynodon* (Murphy, 1977), *B. dendrophila* (Murphy, 1977), *B. multomaculata* (Campden-Main, 1970), *B. trigonata* (Wall, 1907), *Cemophora coccinea* Willard, 1977), *Clelia clelia* (Willard, 1977), *Coluber hippocrepis* (Steward, 1971), *C. viridis* (Steward, 1971), *Conopsis lineatus* (Sajdak, 1976), *Coronella austriaca* (Steward, 1971), *Diadophis punctatus* (Myers, 1965), *Dinodon rufozonatum* (Pope, 1935), *Eirenis modestum* (Klingelhöffer, 1959), *Elaphe diadema* (Willard, 1977), *E. dione* (Steward, 1971), *E. helenae* (Wall, 1913), *E. mandarina* (Golder, 1974), *E. quadrivirgata* (Willard, 1977), *E. quatuorlineata* (Steward, 1974), *E. situla* (Steward, 1971), *E. taeniura* (Boulenger, 1912), *E. vulpina* (Willard, 1977), *Farancia abacura* (Willard, 1977), *F. erythrogramma* Willard, 1977), *Helicops angulatus* (Mole, 1924), *Hemihagererrhis nototaeniatus* (Pitman, 1974), *Hormonotus modestus* (Pitman, 1974), *Lampropeltis mexicanus* (Axtell, 1951), *L.*

zonata (Willard, 1977), *Lamprophis aurora* (Rose, 1955), *L. inornatus* (Rose, 1955), *Leimadophis melanotus* (Mole, 1924), *Lycodon fasciatus* (Wall, 1911), *Lycodonomorphus rufulus* (Rose, 1955), *Lycophidion capense* (Mertens, 1955), *Macroprotodon cucullatus* (Kramer and Schnurrenberger, 1963), *Manolepis putnami* (Werler and Smith, 1952), *Philodryas olfersi* (R. W. Henderson, in litt.), *Psammophis sibilans* (Pitman, 1974), *P. subtaeniatus* (Pitman, 1974), *Pseudaspis cana* (Broadley, 1959), *Pseudoboa coronata* (Mole, 1924), *Pythonodipsas carinata* (Mertens, 1955), *Rhamphiophis oxyrhynchus* (Loveridge, 1928), *Stilosoma extenuatum* (Carr, 1934), *Telescopus dhara* (Pitman, 1974), *T. fallax* (Steward, 1971), *T. semiannulatus* (Pitman, 1974).

APPENDIX B

SAMPLE DATA CHECKLIST

Species _____ Origin, # _____
 Size _____ Observer _____ Date _____
 Live/dead _____ Eyes open/shut _____ Size _____ Color, etc. _____
 Time _____ Temp. _____ Humidity _____ Light _____ cine/videotape/stills/audiotape
 Other _____
PREY in(t): distance: sitting/head move/wash/move fast/slow
 toward/away from snake from snake's left/right/above/front/forceps
SNAKE coil tight/loose neck extended/s-curve crawl fast/slow
 orien(t): 1stTF(t): start move(t): approach(t):
 other _____
STRIKE misses(t): hit(t): tail/rump/torso/shoulder
 neck/head/snout/leg r/l/d/v/a/p/other _____
CONSTRICT start(t): winding/wrapping/mixed/uncertain/shifting _____
 surface used: ventral/L or R lateral/mixed/uncertain/other _____
 part of snake: ant/middle/post/tail/all/other _____
 ventral direction: toward/away/both/intermed/uncertain/other _____
 long axis: horiz/vert/angle _____ prey head up/down snake head up/down
 number of loops: 1/1.5 2/2.5 3/3.5 4/4.5 5/5.5 uncertain/other _____
 prey bites(t): prey moves(t):
PREINGESTION: relax(t): breathe(t): JM(t): release(t): yes/no
 uncoil/pull free(t): recoil(t): TF(t):
 trial bites(t): snout-push(t):
 regrasp(t):
SWALLOWING start(t): uncoil/pull free(t): recoil(t):
 hf/tf/bu/bd/ru/lu front legs(t): hind legs(t): tail base(t):
 finish(t): head-up(t): 1st postingest. RF(t): crawl(t):
 yawn(t):
 NOTES:

ADDITIONAL PREY yes/no

APPENDIX C

LIST OF TAXA STUDIED

Parentheses indicate number of individuals and observations, respectively.

Booidea

Acrochordidae: *Acrochordus javanicus* (1,1).

Aniliidae: *Cylindrophis rufus* (2,3).

Boidae: *Acrantophis dumerili* (2,2), *A. madagascariensis* (1,1),

Aspidites melanocephalus (1,1), *Boa constrictor* (6,29),

Bothrocheilus boa (2,2), *Calabaria reinhardti* (1,7), *Candoia*

bibroni (3,4), *C. carinata* (3,5), *Charina bottae* (1,1), *Chondropython*

viridis (7,7), *Corallus caninus* (4,4), *C. enydris* (7,17), *Epicrates*

angulifer (2,2), *E. cenchria* (11,138), *E. exul* (1,1), *E. gracilis*

(2,7), *E. inornatus* (1,1), *E. striatus* (2,11), *E. subflavus* (1,1),

Eryx jaculus (1,1), *E. johnei* (2,2), *E. tataricus* (1,1), *Eumeces*

murinus (3,23), *E. notaeus* (1,1), *Gongylophis conicus* (1,1), *Liasis*

albertisi (3,3), *L. childreni* (1,1), *L. fuscus* (4,4), *L. mackloti*

(1,1), *L. papuanus* (1,1), *L. boeleni* (1,1), *Lichanura trivirgata*

(1,1), *Loxocemus bicolor* (3,11), *Morelia spilotes* (1,1), *Python*

molurus (6,11), *P. regius* (2,3), *P. timoriensis* (5,5), *Sanzinia*

madagascariensis (2,2).

Tropidophiidae: *Exiliboa placata* (1,1), *Trachyboa boulengeri* (2,2),

Tropidophis canus (5,12), *T. greenwayi* (3,14), *T. haetiianus* (4,9),

Ungaliophis continentalis (1,1), *U. panamensis* (1,1).

Colubroidea

Colubridae: *Arizona elegans* (2,3), *Boaedon fuliginosus* (9,17),
Chrysopelea ornata (1,1), *Elaphe carinata* (2,9), *E. climacophora*
(3,14), *E. flavirufa* (1,1), *E. guttata* (5,9), *E. longissima* (2,4),
E. obsoleta (1,2), *E. radiata* (1,3), *E. schrenki* (2,2),
E. subocularis (3,3), *E. triaspis* (1,1), *Gonyosoma oxycephalum*
(2,5), *Heterodon nasicus* (1,1), *Lampropeltis calligaster* (3,4),
L. getulus (2,4), *L. pyromelana* (2,20), *L. triangulum* (4,78),
Pituophis deppei (1,7), *P. melanoleucus* (2,8), *Pseudoboa*
newwiedii (1,1), *Rhinocheilus lecontei* (1,2), *Spalerosophis*
diadema (2,4), *Spilotes pullatus* (1,11), *Trimorphodon biscutatus*
(4,7), *T. tau* (1,6).

APPENDIX D

SCHEME 1: PATTERNS OF COIL APPLICATION

	<u>Pattern Number</u>
I. Anterior	
A. twist	
1. winding	
a. horizontal	1
b. vertical	2
c. angle	3
d. horizontal/angle	4
e. vertical/angle	5
f. horizontal/vertical	6
2. wrapping	
a. horizontal	7
b. vertical	8
c. angle	9
d. horizontal/angle	10
e. vertical/angle	11
f. horizontal/vertical	12
3. winding/wrapping	
a. horizontal	13
b. vertical	14
c. angle	15
d. horizontal/angle	16
e. vertical/angle	17
f. horizontal/vertical	18
B. no twist	
1. winding	
a. horizontal	19
b. vertical	20
c. angle	21
d. horizontal/angle	22
e. vertical/angle	23
f. horizontal/vertical	24
2. wrapping	
a. horizontal	25
b. vertical	26
c. angle	27
d. horizontal/angle	28
e. vertical/angle	29
f. horizontal/vertical	30
3. winding/wrapping	
a. horizontal	31
b. vertical	32
c. angle	33
d. horizontal/angle	34
e. vertical/angle	35
f. horizontal/vertical	36

C.	twist/no twist	
1.	winding	
a.	horizontal	37
b.	vertical	38
c.	angle	39
d.	horizontal/angle	40
e.	vertical/angle	41
f.	horizontal/vertical	42
2.	wrapping	
a.	horizontal	43
b.	vertical	44
c.	angle	45
d.	horizontal/angle	46
e.	vertical/angle	47
f.	horizontal/vertical	48
3.	winding/wrapping	
a.	horizontal	49
b.	vertical	50
c.	angle	51
d.	horizontal/angle	52
e.	vertical/angle	53
f.	horizontal/vertical	54
II.	Posterior	
A.	twist	
1.	winding	
a.	horizontal	55
b.	vertical	56
c.	angle	57
d.	horizontal/angle	58
e.	vertical/angle	59
f.	horizontal/vertical	60
2.	wrapping	
a.	horizontal	61
b.	vertical	62
c.	angle	63
d.	horizontal/angle	64
e.	vertical/angle	65
f.	horizontal/vertical	66
3.	winding/wrapping	
a.	horizontal	67
b.	vertical	68
c.	angle	69
d.	horizontal/angle	70
e.	vertical/angle	71
f.	horizontal/vertical	72

B.	no twist	
1.	winding	
a.	horizontal	73
b.	vertical	74
c.	angle	75
d.	horizontal/angle	76
e.	vertical/angle	77
f.	horizontal/vertical	78
2.	wrapping	
a.	horizontal	79
b.	vertical	80
c.	angle	81
d.	horizontal/angle	82
e.	vertical/angle	83
f.	horizontal/vertical	84
3.	winding/wrapping	
a.	horizontal	85
b.	vertical	86
c.	angle	87
d.	horizontal/angle	88
e.	vertical/angle	89
f.	horizontal/vertical	90
C.	twist/no twist	
1.	winding	
a.	horizontal	91
b.	vertical	92
c.	angle	93
d.	horizontal/angle	94
e.	vertical/angle	95
f.	horizontal/vertical	96
2.	wrapping	
a.	horizontal	97
b.	vertical	98
c.	angle	99
d.	horizontal/vertical	100
e.	vertical/angle	101
f.	horizontal/vertical	102
e.	winding/wrapping	
a.	horizontal	103
b.	vertical	104
c.	angle	105
d.	horizontal/vertical	106
e.	vertical/angle	107
f.	horizontal/vertical	108

III. Anterior/posterior

A. twist

1. winding
 - a. horizontal 109
 - b. vertical 110
 - c. angle 111
 - d. horizontal/angle 112
 - e. vertical/angle 113
 - f. horizontal/vertical 114
2. wrapping
 - a. horizontal 115
 - b. vertical 116
 - c. angle 117
 - d. horizontal/angle 118
 - e. vertical/angle 119
 - f. horizontal/vertical 120
3. winding/wrapping
 - a. horizontal 121
 - b. vertical 122
 - c. angle 123
 - d. horizontal/angle 124
 - e. vertical/angle 125
 - f. horizontal/vertical 126

B. No twist

1. winding
 - a. horizontal 127
 - b. vertical 128
 - c. angle 129
 - d. horizontal/angle 130
 - e. vertical/angle 131
 - f. horizontal/vertical 132
2. wrapping
 - a. horizontal 133
 - b. vertical 134
 - c. angle 135
 - d. horizontal/angle 136
 - e. vertical/angle 137
 - f. horizontal/vertical 138
3. winding/wrapping
 - a. horizontal 139
 - b. vertical 140
 - c. angle 141
 - d. horizontal/angle 142
 - e. vertical/angle 143
 - f. horizontal/vertical 144

C. Twist/no twist	
1. winding	
a. horizontal	145
b. vertical	146
c. angle	147
d. horizontal/angle	148
e. vertical/angle	149
f. horizontal/vertical	150
2. wrapping	
a. horizontal	151
b. vertical	152
c. angle	153
d. horizontal/angle	154
e. vertical/angle	155
f. horizontal/vertical	156
3. winding/wrapping	
a. horizontal	157
b. vertical	158
c. angle	159
d. horizontal/angle	160
e. vertical/angle	161
f. horizontal/vertical	162

APPENDIX E

SCHEME 2: PATTERNS OF COIL APPLICATION

<u>Characteristics</u>	<u>Pattern Number</u>
I. Anterior	
A. twist	
1. winding	1
2. wrapping	2
3. winding/wrapping	3
B. no twist	
1. winding	4
2. wrapping	5
3. winding/wrapping	6
C. twist/no twist	
1. winding	7
2. wrapping	8
e. winding/wrapping	9
II. Posterior	
A. twist	
1. winding	10
2. wrapping	11
3. winding/wrapping	12
B. no twist	
1. winding	13
2. wrapping	14
3. winding/wrapping	15
C. twist/no twist	
1. winding	16
2. wrapping	17
3. winding/wrapping	18
III. Anterior/posterior	
A. twist	
1. winding	19
2. wrapping	20
3. winding/wrapping	21
B. no twist	
1. winding	22
2. wrapping	23
3. winding/wrapping	24
C. twist/no twist	
1. winding	25
2. wrapping	26
3. winding/wrapping	27

VITA

Harry Walter Greene was born in Detroit, Michigan, on September 26, 1945. He attended elementary and secondary schools in five states and the Philippine Islands. He received a diploma from Eastern Hills High School of Fort Worth in 1963, a Bachelor of Science degree in Biology from the University of Texas at Arlington in 1973, and a Doctor of Philosophy degree in Zoology from the University of Tennessee in 1977. During graduate school he worked as a museum research assistant and a teaching assistant. Mr. Greene has done field work in the United States, Europe, Mexico, Guatemala, and Panama. His accomplishments include over 20 publications, the 1973 Best Student Paper Award for the Journal of Herpetology, the 1974 Outstanding Graduate Student Award at the University of Tennessee, and a 1977 Chancellor's Citation for Extraordinary Academic Achievement. His research interests are in evolutionary biology, especially the behavior, ecology, and comparative morphology of vertebrates. He likes Thomas Wolfe, Vincent Van Gogh, Fleetwood Mac, animals, sunrises, old clothes, new places, and a woman with high cheekbones.