compared to the males where maximum 'sparing effect' in terms of increase in life span is only around 12%. It has been demonstrated that the colony-forming ability of cultured mammalian cells exposed to radiation given in 2 equal fractions was maximal if the interval between the 2 fractions was 2-3 h, declined slightly with somewhat longer intervals, and in some cases it rose again when the intervals were much longer. This phenomenon, often referred to as 'Elkind kinetics'[14], demonstrates that there is one very rapid and another much slower phase of repair of radiation injury, and that repair is at the subcellular level, since in cell cultures there was no opportunity for cell replacement.

Studies with varying interfraction intervals reveal that maximum sparing effect in females of dose-fractionation is obtained with an interval of 18 h (table). The LD50 values are about 12.5 and 16.2 days for 60 krad delivered in single and split-dose respectively. Kinetics of recovery through dose-fractionation was analyzed in *Tribolium confusum* where maximum recovery was obtained with 5 h interval[15]. Adult male *Drosophila* is considered to be a predominantly postmitotic system compared to females which have dividing cells associated with ovarian development. In the current experiments, maximum recovery has been observed in the females, which implies that the dividing cells associated with ovarian development are able to repair efficiently.

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Behavioral convergence in the defensive displays of snakes[1]

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Summary. Comparison of habitats and defensive displays in 129 species suggests convergent behavioral evolution. In snakes, antipredator tactics are apparently superimposed at the population, species, or generic level on much older adaptations for feeding.

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? These important evolutionary problems[2-4] have rarely been addressed from a rigorous comparative perspective, perhaps because it is difficult to obtain large and diverse enough samples of taxa to be informative. Here I summarize observations and literature on 129 species of snakes (77 genera, 5 families) that exhibit 3 widespread types of defensive displays. The goal is to distinguish between ancient and recent origins of behavioral similarity by searching for phylogenetic or ecological correlations[5,6].

Methods. Genera were used in this analysis, with 1 exception, because all species in most genera used the same display type and because the 16 species of *Micrurus* would bias the comparison. 5 species of *Oligodon* use tail displays; *O. arnensis* uses a head display and was scored separately. *Drymarchon*, *Erythrolamprus*, and *Heterodon* were excluded because they each use 2 display types. The remaining 75 taxa were classified as a) fossorial and/or terrestrial or b) arboreal or semiarboreal. Tail displays are postural shifts in which the tail is made more prominent than it is in a normal resting posture or locomotion. This can consists of elevating and in some cases coiling and waving the tail back and forth. A vertical head display increases the dorsoventral dimension by laterally compressing and/or inflating the anterior part of a snake's body. This often also includes drawing back the anterior part of the body into an exaggerated S-shaped coil, spreading the posterior part of the head, and opening the mouth. A horizontal head display increases the lateral dimension by dorsoventrally flattening

the anterior part of the snake's body. This is often accompanied by elevation of the head and anterior part, and sometimes by holding the mouth open. For descriptions of individual taxa see[6-8].

Results and discussion. The table demonstrates that display types are significantly associated with habitat classes. Factors selecting for the repeated evolution of similar displays remain to be studied, but could include characteristics of the snakes, their predators, or their interactions peculiar to each habitat.

Tail displays are almost entirely restricted to terrestrial or fossorial snakes (97.6% of 42 genera with this behavior). These are assigned to the Aniliidae, Boidae, Colubridae, Elapidae, and Viperidae, and the latter 4 families also include arboreal species that do not use tail displays. It is possible that the similar displays of aniliids and boids are shared primitive behavior patterns that were present in ancestral snakes. However, the burrowing colubrid and elapid genera almost certainly resulted from numerous independent derivations from a generalized terrestrial colu-

Relationship of habitat to defensive display behavior in 75 snake taxa (χ^2, $p < 0.01$)

Habitat	Tail display	Vertical head display	Horizontal head display
Fossorial or terrestrial	38	3	20
Arboreal or semiarboreal	1	13	0

A   B
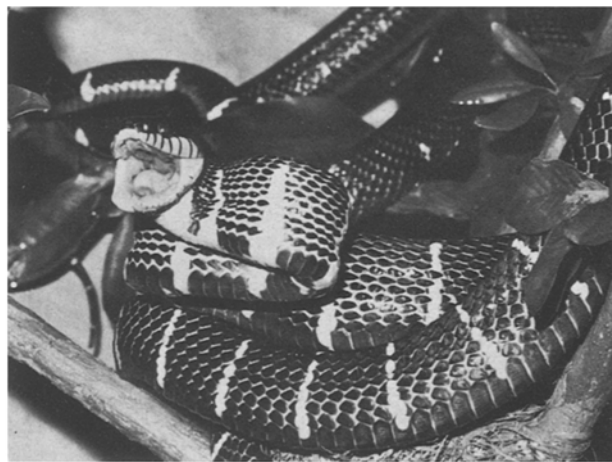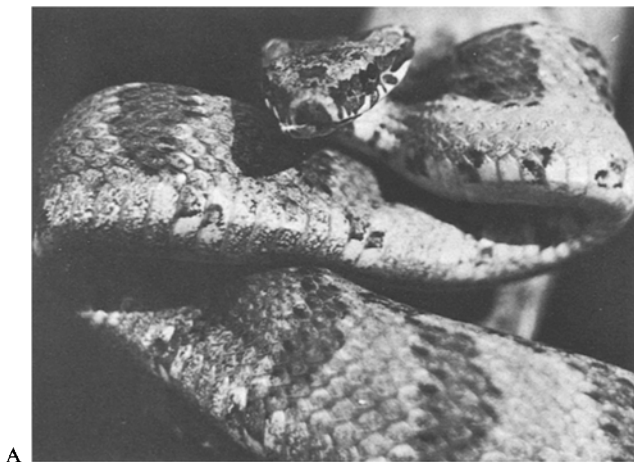
Defensive displays of *Pseustes poecilonotus* (A) from Panama and *Boiga dendrophila* (B) from southeastern Asia.

broid[9], and it is thus very likely that the similarities among their defensive displays are due to convergence. This conclusion is strengthened by a more detailed consideration of 3 genera. African mole vipers *(Atractaspis)* are small (< 1 m total length) burrowing snakes that feed on lizards, snakes, and mammals. Their defensive behavior includes hiding the head, flattening and erratically snapping the body, elevating and curling the tail, and biting[10]. Venomous coral snakes *(Micrurus)* are small (usually < 1 m total length), inhabit forest litter, and feed on elongate vertebrates. Their defensive behavior is virtually identical to that of *Atractaspis*, except that the somewhat longer tail of *Micrurus* is often coiled in a loop when it is elevated. False coral snakes *(Erythrolamprus)* are similar in size, coloration, and ecology to *Micrurus*. They have similar defensive behavior, except that the anterior part of the body of *Erythrolamprus* is sometimes also flattened and elevated. *Atractaspis, Erythrolamprus,* and *Micrurus* are not closely related, are approximate ecological equivalents, and have very similar, probably convergently evolved defensive displays.

Vertical head displays predominate among arboreal snakes (92.9% of 14 genera), and are much less common among terrestrial taxa (4.9% of 61 genera). The arboreal colubrids include 8 Old World and 5 New World genera. With 2 possible exceptions *(Pseustes* and *Spilotes, Dispholidus* and *Thelotornis)*, I know of no evidence of close relationships among them; they would be placed in at least 4 subfamilies in a recent classification of colubrids[11]. It is therefore likely, at least in most instances, that the similarities in defensive displays among these genera are due to convergence and not to common ancestry. A more refined comparison between 2 species underscores this conclusion. *Pseustes poecilonotus* is a large (about 2 m), diurnal, arboreal, neotropical rain forest snake that feeds on birds and mammals. The defensive display includes lateral compression of the body, inflating the anterior trunk, spreading and depressing the mandibles, and striking (figure, A). The overall effect to a human observer is to greatly increase the apparent size of the anterior part of the snake, and perhaps to increase resemblance to a venomous pit viper[12]. *Boiga dendrophila* of southeastern Asia is morphologically and ecologically similar to *P.poecilonotus*. It is a large (about 2 m) nocturnal, arboreal, rain forest inhabitant that feeds on birds and mammals. The defensive display (figure, B) is extremely similar to that of *P.poecilonotus* in terms of the component postures and their approximate order of appearance. There is no evidence that these 2 species are closely related, and they are usually assigned to different subfamilies[11,13].

Horizontal head displays are restricted to terrestrial species in 13 Old World and 9 New World genera. These represent the Colubridae, Elapidae, and Viperidae, and the colubrids are assigned to at least 5 subfamilies[11,13]. Given the taxonomic and geographic diversity represented by the 22 genera, much of the similarity in defensive behavior must be due to convergence.

A concurrent survey of constricting coil application behavior among 45 species (4 families) of primitive snakes demonstrated that a very similar action pattern was probably used by their common ancestor in the Cretaceous[14]. In contrast, defensive tail displays are largely restricted to small or medium length burrowing species in this group. Taken together, these studies imply that antipredator tactics are rather tightly coupled to the predation problems faced by a population at a particular time and place, and that they are superimposed on much older and more widespread adaptations for feeding. Future comparisons among other taxa might lead to a comprehensive theory incorporating different animals and different kinds of behavior.

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