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## Individual variation in the antisnake behavior of California ground squirrels (*Spermophilus beecheyi*)

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# INDIVIDUAL VARIATION IN THE ANTISNAKE BEHAVIOR OF CALIFORNIA GROUND SQUIRRELS (*SPERMOPHILUS BEECHEYI*)

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California ground squirrels (*Spermophilus beecheyi*) have evolved behavioral defenses against their two predators, the northern Pacific rattlesnake (*Crotalus viridis oreganus*) and Pacific gopher snake (*Pituophis melanoleucus catenifer*). Two studies were used to examine individual variation in antisnake behavior as it might be affected by selection operating on arousability, fearfulness, and aggressiveness. In Study 1 the behavioral consistency of two litters of lab-reared juveniles was examined at two age periods during encounters with a caged gopher snake and domestic cat. Close-range investigation and tail flagging appeared to be governed by short-term motivational states that were not strongly correlated across age. Age correlations revealed that individual tendencies to throw substrate were relatively consistent for the snake and even more so for the cat. In Study 2, wild-caught adults were obtained from five sites where rattlesnakes and gopher snakes were abundant and from five sites where these snakes were rare or absent. Squirrels in a seminatural laboratory setting were given balanced presentations of a caged rattlesnake and gopher snake separated by 5 days. Snakes were recognized by all squirrels as potentially dangerous, irrespective of experience, age, and selective regime. Substrate throwing also was positively correlated for the two snakes in both groups of adults, indicating that level of aggressiveness is a consistent component of temperament not specific to species of snakes. Physiological arousal was not correlated strongly for the two snakes, but it was significantly lower in squirrels from sites where snakes were abundant. This suggests some specialization to reduce anxiety that possibly enhances tactical decision making.

**Key words:** *Spermophilus beecheyi*, antipredator behavior, canonical correlation analysis, gopher snakes, ground squirrels, individual variation, rattlesnakes, temperament

The view that individuals within a population are adapted to deal with a specific environmental problem assumes that the problem is definable and recurrent historically. As Mayr (1976) emphasized repeatedly, such characterization of adaptive processes is an a posteriori procedure that relies on the accumulation of information about the interplay of ecological, physiological, and behavioral variables (Krimbas, 1984). For any complex organism-environment problem, individual variation in performance reflects the constraints that emerge in the dynamic interplay of these variables and the stochastic properties inherent in their relationships.

In this paper, we examine individual variation in how California ground squirrels (*Spermophilus beecheyi*) cope with two predators, the northern Pacific rattlesnake (*Crotalus viridis oreganus*) and Pacific gopher snake (*Pituophis melanoleucus catenifer*). In Study 1, we observed juveniles at two age periods to examine consistency in snake-directed behavior. In Study 2, we examined properties of individual variation in antisnake behavior in a set of populations with different histories of predation from snakes. In both studies, monitoring individual consistency in behavior provided insight into how selection might operate on antisnake behavior.

*Historical stability of squirrel-snake interactions.*—The ancestors of *S. beecheyi* have likely been targets of predation by *C. viridis* and *P. melanoleucus* for thousands of years. Sympatry of ground squirrels with both species of snakes in northern California is clearly evident in fossil assemblages that span most of the Pleistocene (Miller, 1912; Poran and Coss, 1990; Stock, 1918). Much older contact between rattlesnakes and the *Otospermophilus* progenitor of modern ground squirrels and prairie dogs can be inferred from the temporal and regional contiguity of middle-Miocene fossil deposits (Black, 1963; Holman, 1979).

The historical abundance of ground squirrels has shaped the dietary preference of rattlesnakes and gopher snakes that hunt ground squirrels, especially the young (Fitch, 1948, 1949). *S. beecheyi* counters this predation by engaging in a variety of antisnake behaviors, including close-range harassment, that might thwart predation by rattlesnakes (Owings and Coss, 1977). Despite their hazards, confrontational tactics can clearly disrupt the activity of a rattlesnake or gopher snake and might spur these snakes to hunt elsewhere. Such behaviors can include pouncing on and biting the rattlesnake (Owings and Coss, 1977), but more commonly consist of prolonged staring and peppering the snake with loose substrate vigorously thrown by the forepaws, a process that can deflect strikes (Coss, 1991a; Coss and Owings, 1978, 1989). The conspicuous tail flagging noted by Fitch (1948) is a highly variable signal with multiple functions, including attracting the snake's attention (Hennessy et al., 1981; Hennessy and Owings, 1988; Hersek and Owings, 1993, 1994).

Cautious investigation of snakes by *S. beecheyi* is clearly regulated by situational stochasticity, that is, whether the snake was detected initially at a safe distance. Rattlesnakes in defensively coiled postures generally are approached more cautiously than when mobile and, therefore, less able to retaliate (Coss and Owings, 1989). Careful

regulation of distance from coiled snakes suggests that squirrels are cognizant of the dangerous operating range of these slow-moving predators (Coss, 1993). Excluding sudden encounters and ambushing events by rattlesnakes and gopher snakes that engender evasive behavior, squirrels can investigate snakes for prolonged periods by staying outside of striking range (Rowe and Owings, 1990). It is, therefore, reasonable to assert that the risky properties of engaging snakes in this manner have been ecologically stable for thousands of years.

*Stability of snake-recognition system.*—The historically stable properties of morphology of snakes have promoted the evolution of a generalized snake-recognition system in *S. beecheyi*. Visual detection of stationary rattlesnakes or gopher snakes should be difficult because both snakes exhibit similar cryptic patterning (Cott, 1940; Sweet, 1985). Yet, ground squirrels are capable of detecting motionless snakes embedded in diverse textures of leaf litter and detritus from distances >10 m. Moreover, young, newly emerged from natal burrows at ca. 45 days of age, quickly adopt adult-like, elongate, investigative postures and tail flag after they detect an immobile rattlesnake. They also cautiously approach long sticks that superficially resemble snakes (Coss 1991a; Poran and Coss 1990). Experimental study of the developmental onset of recognition of gopher snakes in two litters of young showed that innate olfactory processes are functional around the time of eye opening, at 33–39 days of age, when sensory projections to the brain are established (Coss, 1991b). In older individuals, olfactory cues are used to distinguish rattlesnakes from gopher snakes, especially in burrows (Hennessy and Owings, 1978; Towers and Coss, 1990). Further longitudinal study of these young revealed that innate visual recognition of a gopher snake had a sharp onset at 40–41 days of age, the first day young showed evidence of pattern vision (Coss, 1991a).

*Behavioral organization.*—Although every *S. beecheyi* examined in detail in previous studies in both field and laboratory settings recognized snakes as dangerous, their subsequent action patterns were highly variable. Pausing, evasive leaping, and substrate throwing are single behavioral actions tightly coupled with the initial phase of recognition of snakes. Whereas these defensive tactics have some automaticity in their expression, they are not unique to encounters with a snake and squirrels regulate their application depending on circumstances of the microhabitat (Coss, 1993; Coss and Owings, 1985). Their application in an urgent context provides a brief temporal window in which selection can act on differential outcomes.

It is less clear how selection would act on different sequences of action patterns with multiple functions organized in a longer time domain. While tail flagging has multiple functions uniquely related to dealing with snakes, elongate postures and substrate throwing have much broader utility as investigative behaviors. In other rodents, hesitant approaches with elongate postures, elevated tails, and substrate throwing are coupled together as a common suite of highly conserved behaviors during the cautious investigation of something snakelike (e.g., Heynen, et al., 1989). For example, lab-born Arctic ground squirrels (*S. parryii*) from snake-free central Alaska did not throw substrate at a caged rattlesnake, nor did they recognize snakes as dangerous (Coss and Goldthwaite, 1995; Goldthwaite, 1989). However, several individuals threw substrate vigorously at a caged domestic cat that superficially resembled their natural predator, the Canadian lynx (*Lynx canadensis*). Substrate pushing and throwing with forepaws and hind paws also has general utility for excavation of burrows and debris clearing. Its application against snakes probably originated as an antipredator tactic for dealing with burrow intruders (Goldthwaite et al., 1990).

When a ground squirrel and snake inter-

act, the unfolding relationship can be viewed as a dynamic system restricted by microhabitat features, but constantly adjusted by the interplay and feedback of the activities of both parties. A major difficulty in evaluating individual variation in this type of dyadic relationship is determining whether the underlying behavior should be characterized as discrete units or as composite units at higher levels of spatial and temporal organization (Fentress, 1987; Timberlake and Silva, 1995). Both discrete and composite units of behavior emerging in this interaction would be regulated by the interplay of developmentally stable and labile processes involving the temperaments, motivational states, and experiences of both individuals (for rattlesnakes see Marmie et al., 1990). Antisnake behavior of ground squirrels is much less amenable to system characterization than highly organized, self-directed, activities lacking extrinsic threats. For example, autogrooming exhibits an innate syntactic chaining of single-action patterns (Berridge, 1990, 1994). For natural selection to operate on the larger spectrum of sequential antisnake behaviors unfolding in time, higher-order stability in organization of motor-patterns must emerge, yielding outcomes that promote fitness. With this in mind in Study 2, we have examined individual variation in the cohesive properties of behavior directed toward defensive snakes.

*Personality differences.*—Temperament typically is considered a developmentally stable component of an animal's personality that varies considerably among individuals. Its stability is revealed by consistent behavioral activity evaluated by longitudinal study (Lyons et al., 1988) or by correlating behaviors that reveal similar tolerance to stress. In male threespine sticklebacks (*Gasterosteus aculeatus*), for example, aggressiveness in territorial defense is positively correlated with boldness in inspection of the predator (Tulley and Huntingford, 1988). Under less predictable conditions, individuals with lower reactivity of the

sympathetic nervous system might be able to cope more effectively with variable situations than more jumpy individuals (Benus et al., 1991). For example, Whitney (1970) found differences between strains in the effects of loud noise on the open-field behavior of inbred laboratory mice. The most fearful genotype exhibited surprisingly less timidity during emergence from the home cage than the least fearful genotype, which showed much more caution in this uncertain environment.

To summarize with relevance to *S. beecheyi*, this theoretical perspective leads to the prediction that individuals intolerant of both emotional arousal and uncertainty would be risk averse and, therefore, less likely to confront snakes. If confrontational tactics are indeed adaptive, then directional selection might suppress the emotional aversiveness of engaging snakes, possibly enhancing tactical decision making that reduces the likelihood of envenomation. For assessing the emotional states of *S. beecheyi* in this context, the degree of tail piloerection provides a reliable index of arousal of the sympathetic nervous system (Fuchs et al., 1985; Rowe et al., 1986; Siegel and Skog, 1970). In addition, motivational changes associated with reproductive status also can affect the willingness of females to engage rattlesnakes (Swaigood, 1994).

*Experimental objectives.*—The major focus of the present research was to study individual variation in antisnake behavior that might be subject to selection. We emphasized behavioral measures possibly affected by the three aforementioned facets of temperament; arousability, fearfulness, and aggressiveness. It is still unclear from previous studies whether reactivity of the sympathetic nervous system is a generalized temperamental component of personality or has specialized aspects unique for coping with different snakes as predators. If reactivity of the sympathetic nervous system is a core component of personality unaffected by specific threatening circumstances, then squirrels whose ancestors ex-

perienced strong selection by snakes should not differ appreciably in arousability from squirrels whose ancestors experienced prolonged relaxed selection from snakes.

Individual variation in sustained vigilance and willingness to approach snakes closely might shed light on level of fearfulness. Aggressiveness can be evaluated directly via substrate throwing as an act of boldness in probing and harassing snakes. Tail flagging has multiple functions, especially communicative, that could be linked to any of the three facets of temperament selected for study.

We conducted two studies to address these issues. In the first, we examined longitudinal changes in the behavior of lab-born, juvenile, *S. beecheyi* from a single population. In Study 2 we documented individual variation in the behavioral organization of wild-caught *S. beecheyi* during encounters with a caged rattlesnake and gopher snake. The primary goal of this study was comparing squirrels from sites where rattlesnakes and gopher snakes were abundant with squirrels from sites where these snakes were rare or absent.

## STUDY 1

*Subjects.*—Two pregnant California ground squirrels trapped at Folsom Lake State Recreation Area, Eldorado Co., California, gave birth to two litters on the same day. Rattlesnakes and gopher snakes are abundant around the lake, although virtually absent at the trapping site due to boat-launching activity. Squirrels from this site are strongly resistant to rattlesnake venom (Poran et al., 1987; Towers and Coss, 1990). Young within litters were presumed to have been fathered by several different males (Boellstorff et al., 1994). One juvenile died during weaning, yielding six (litter 1) and four (litter 2) juveniles for comparisons of litter and age.

We tested 10 juveniles at 76–77 days of age (mean = 366,  $SD = 48$  g) and again at 89–90 days of age in the same experimental setting previously used to determine the onset of recognition of snakes (Coss, 1991a). Each juvenile was released from a transfer box into a white experi-

ment chamber (0.90 m high by 1.22 by 0.57-m floor) with a transparent plexiglas wall for videotaping behavior from an adjacent room via a one-way mirrored window. We released squirrels ca. 10 cm away from a 28 by 28 by 28-cm compartment centered against the back wall, which contained either a Pacific gopher snake (snout-vent length, 98 cm; body weight, 416 g) or a domestic cat. Each potential predator was clearly visible through the compartment's 8-mm-gage, wire-screen, mesh (Coss, 1993). Behavior of squirrels was videotaped from the side view for a 5-min trial. One predator was presented in the morning and the second predator was presented in the afternoon in a balanced order, ca. 3 h later. Squirrels were readily retrieved after each trial using the familiar transfer box and returned to their home cages.

Four behaviors employed in investigation of snakes were examined for age-related stability. These were: 1) total duration (s) that the juvenile's tail was elevated above the body (with base of tail minimally ca. 90° perpendicular to the spine's axis in perspective view); 2) number of investigative approaches; 3) number of substrate-throwing acts; 4) number of tail-flagging cycles. Tail elevation was considered a proxy measure of general excitability (Coss, 1991a), but it often has been observed as a prelude to tail flagging after detection of a snake. Additional behaviors more relevant to dealing with unfamiliar mammals were: 5) duration of bipedal standing and upright sitting posture (s); 6) duration of digging (s); 7) number of bouts where juveniles inspected the faces of the caged animals.

## RESULTS

Juveniles quickly adopted elongate postures during trials with the gopher snake; they appeared more relaxed while investigating the cat. None of the squirrels attempted to escape the experiment chamber in any trial. Because the gopher snake and cat monitored the approaching squirrels, close inspection by squirrels typically was directed at the predator's face. Although substrate throwing as probing occurred less often during presentations of the cat, this appeared to be context specific. Two fe-

males that passively monitored the gopher snake threw substrate vigorously at the dark entrance of their transfer box after the gopher snake was removed (Coss, 1993:180, figure 3).

We used one-factor between groups (litters), two-factor within groups (age and predators), repeated-measures analyses of variance to examine differences in the gopher snake and cat treatments at 76–77 and 89–90 days of age. Tests of simple effects and planned comparisons identified specific differences within and between litters. We used Pearson product-moment correlations with Bonferroni probabilities to examine age-related behavioral continuity and the relationships of variables within each age class.

Averaged for both litters and age, the gopher snake engendered a significantly greater duration of tail elevation than that of the cat (main effect:  $F = 8.243$ ,  $df. = 1,8$ ,  $P < 0.025$ ). Litter 1 showed a marked decline in tail elevation at 89–90 days of age, averaged for both predators, and a significantly lower duration of tail elevation than litter 2 (simple effect:  $F = 7.424$ ,  $df. = 1,8$ ,  $P < 0.05$ ). Difference between litters in tail elevation at this age was most pronounced (Fig. 1A) during interactions with the gopher snake (planned comparison:  $F = 5.725$ ,  $df. = 1,8$ ,  $P < 0.05$ ). Correlation of individual tail elevation at the two ages revealed that squirrels were inconsistent in the presence of the snake ( $r = 0.366$ ); however, tail elevation was much more consistent during the presentations of the cat ( $r = 0.876$ ,  $P < 0.005$ ).

The gopher snake was approached closely significantly more frequently than the cat, averaged for both litters and age (main effect:  $F = 6.151$ ,  $df. = 1,8$ ,  $P < 0.05$ ). There was a strong litter-by-age interaction ( $F = 23.947$ ,  $df. = 1,8$ ,  $P < 0.005$ ). The primary source of this interaction (Fig. 1B) was the significantly greater frequency at which litter 2 investigated both predators compared with litter 1 at

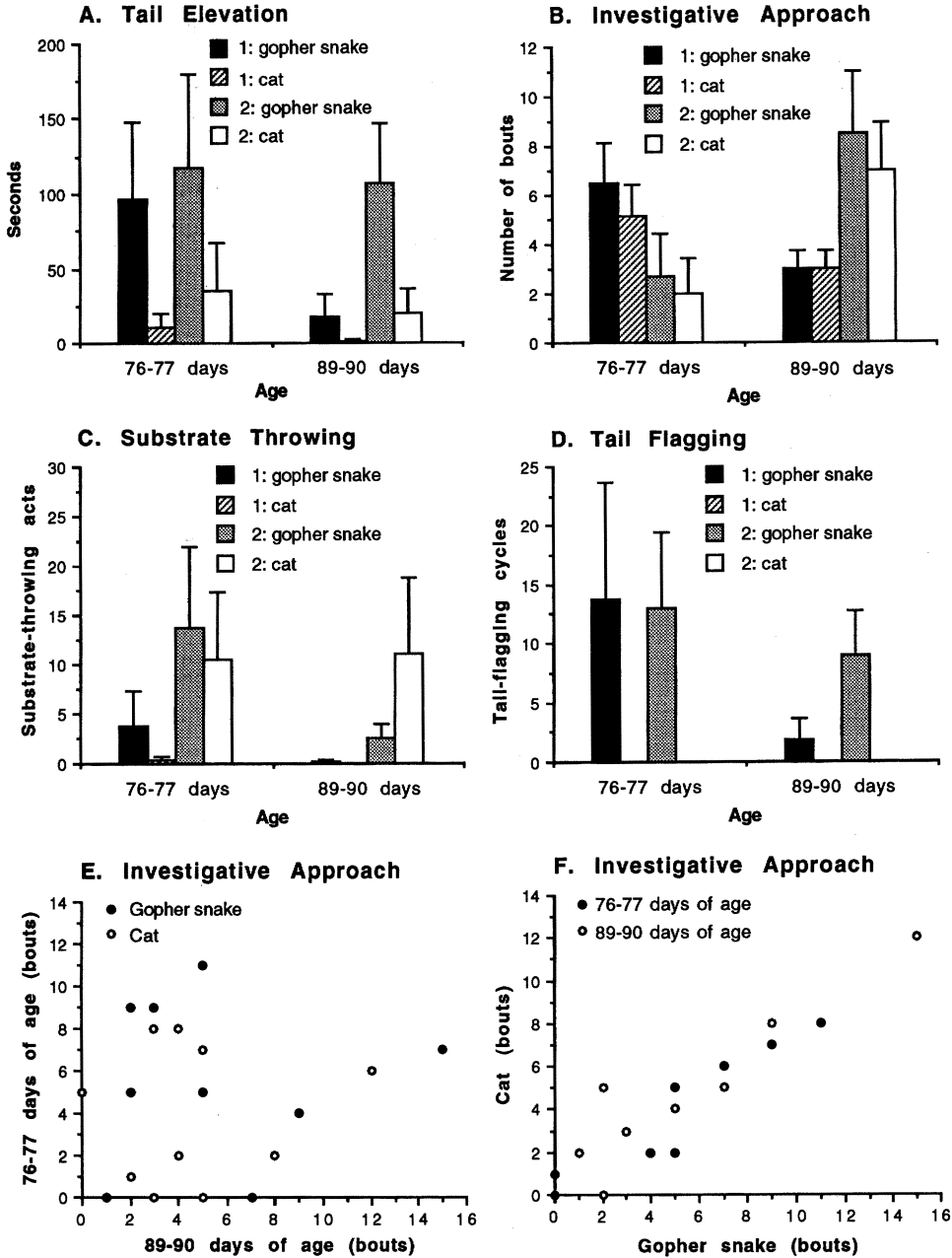


FIG. 1.—Behavior of two litters of juvenile ground squirrels at 76–77 and 89–90 days of age during interactions with a caged gopher snake and domestic cat. Means and standard errors are shown and numbers in figure legends denote the two litters. Ground squirrels differentiated ( $P < 0.05$ ) the gopher snake from the cat in their tail elevation (A), investigative approach (B), and tail flagging (C). Litters differed appreciably at the oldest age for tail elevation (A) and investigative approach (B), and in substrate throwing at both age classes (C). Correlations of investigative approach do not show consistency across age classes (E), but are consistent for both predators for the same day (F).

89–90 days of age (simple effect:  $F = 6.167$ ,  $d.f. = 1,8$ ,  $P < 0.05$ ). Age correlations (Fig. 1E) did not reveal behavioral continuity for presentations of the snake and cat ( $r = 0.103$ ,  $0.098$ , respectively). Although variable across age, squirrels on the same day (Fig. 1F) were consistent in approaching each predator a similar number of times (76–77 days of age:  $r = 0.953$ ,  $P < 0.001$ ; 89–90 days of age:  $r = 0.925$ ,  $P < 0.001$ ).

Litters differed significantly in substrate throwing, averaged for both predators (main effect:  $F = 6.049$ ,  $d.f. = 1,8$ ,  $P < 0.05$ ), a property most apparent at 89–90 days of age (simple effect:  $F = 5.318$ ,  $d.f. = 1,8$ ,  $P = 0.05$ ). Substrate-throwing activity on average declined with age (Fig. 1C), mostly for members of the first litter. Although correlations with age were positive for the snake ( $r = 0.738$ ,  $P = 0.089$ ) and even more so for the cat ( $r = 0.993$ ,  $P < 0.005$ ), individuals were inconsistent in throwing substrate at the two predators the same day ( $r = 0.033$ – $0.198$ ).

Tail flagging only occurred during presentations of snakes (main effect:  $F = 6.891$ ,  $d.f. = 1,8$ ,  $P < 0.05$ ) in keeping with its specificity for dealing with snakes. There were no significant age or litter differences in this behavior (Fig. 1D). Little continuity in tail-flagging activity was evident across ages during presentations of gopher snakes ( $r = 0.117$ ). In both age classes, the duration of tail elevation was positively correlated with tail-flagging activity, suggesting some coupling between these behaviors (76–77 days of age:  $r = 0.900$ ,  $P < 0.01$ ; 89–90 days of age:  $r = 0.985$ ,  $P < 0.001$ ). The additional behavioral measures of face inspection, bipedal posture, and digging were not appreciably different for the two predators. These behaviors were also not consistent across ages.

## STUDY 2

*Subjects.*—We caught 40 adults at five sites where rattlesnakes and gopher snakes were abundant and 40 adults at five sites where these

snakes were rare or absent ( $n = 8$  adults/site, about balanced for sex). Based on range maps and latent resistance to venom as a physiological index of predation by rattlesnakes (Coss and Goldthwaite, 1995), we chose squirrels from the following snake-selected sites in California: Folsom Lake Reservoir in the foothills of the Sierra Nevada Mountains; Walnut Creek, Willows, and Winters in the foothills of the eastern Coast Range; in the foothills at the eastern base of the Coast Range near Tracy. These populations exhibit moderate to high levels of resistance to venom inferred from serum-to-venom binding (Coss et al., 1993; Poran et al., 1987). Sites in California under relaxed selection were Petaluma in the foothills of the western Coast Range, Lake Tahoe Basin in the Sierra Nevada Range, and Mount Shasta in the Cascade Range. Sites in Oregon under relaxed selection were Logsdan near Newport in the foothills of the western Coast Range and Finley National Wildlife Refuge near Corvallis at the base of the foothills in the eastern Coast Range. All five populations exhibit low serum-to-venom binding (Poran et al., 1987; Towers and Coss, 1990).

*Methods.*—We videorecorded close-range interactions between ground squirrels and snakes from an overhead view using an experiment room (2.53 m high by 2.43 m by 2.90-m floor) with a 5-cm-deep layer of sand to provide a natural substrate. To facilitate videorecordings, the room was provided with a convex mirror (44-cm diameter) suspended from the ceiling and a one-way mirrored window to an adjacent studio room (Coss, 1991a). Eight squirrels from each site were permitted to live in the experimental setting for several weeks prior to exposure to a rattlesnake and gopher snake. One hour before presenting each species of snake, we sealed all squirrels in their wire-screened nest boxes and removed them from the room, except the experimental subject, which remained in a bottomless, wooden, nest box that could be raised remotely to release the squirrel. A Pacific gopher snake (snout-vent length = 99 cm; body weight = 465 g) or a northern Pacific rattlesnake (snout-vent length = 82 cm; body weight = 592 g) was placed in the 28 by 28 by 28-cm, wire-screened compartment with transparent plexiglas top used in Study 1. This cage was designed to protect both animals during the encounter and simulated a natural behavioral context in which the coiled



snake held its ground (Coss, 1991a; Coss et al., 1993).

We presented each snake once in a balanced order for a 5-min trial that began with the onset of recognition of the snake as evidenced by tail piloerection. Presentations were separated by a 5-day interval to minimize possible carry-over effects. The compartment housing the snake was positioned in the center of the room seconds before releasing the squirrel. After the nest box was raised, the ground squirrel typically froze for a short period and then approached the cage that superficially resembled its wire-screened nest box.

Teams of two investigators decoded the videotapes to quantify the following behavioral variables. 1) We determined the percentage of instantaneous time-samples (at 10-s intervals) in which the squirrel's head was within the 56-cm radius of the compartment's center. This distance defined the approximate maximum striking range of the rattlesnake (roughly one-third of the snake's length—Klauber, 1972; Rowe and Owings, 1990). The width of the compartment was employed as a scale reference for all time-sampled measures and the percentage scores were transformed into arcsine values for statistical analyses. 2) We used tail piloerection as an index of arousal of the sympathetic nervous system. Maximum tail width was measured from individual video still fields at 10-s intervals when the squirrel's head was within the 56-cm radius and averaged for the trial. 3) We measured the total duration (s) that the squirrel faced the center of the compartment from any location in the experiment room. Facing was defined as the approximate intersection of the orientation of the sagittal plane of the squirrel's head with the compartment's center. Measurements using stop-watches were averaged and repeated if they deviated by  $>2$  s throughout the 5-min trial. 4) We counted total number of substrate-throwing acts directed at the snake and 5) we counted total number of tail-flagging cycles.

## RESULTS

Every squirrel adopted an elongate posture with tail piloerection and became jumpy after detecting the caged snake centered in the laboratory room. Most squirrels employed tail flagging and nearly all squirrels threw substrate, sometimes jumping

sideways immediately afterward as if anticipating that the typically motionless snake suddenly would lunge forward. Univariate descriptions of mean differences between snake-selected and relax-selected groups are summarized elsewhere (Coss, in press; Coss and Goldthwaite, 1995), but are reviewed here briefly to provide the context for correlational analyses. Averaged for both snakes, squirrels in the relax-selected group were significantly more aroused physiologically ( $P < 0.0001$ ) and more vigilant, as evidenced by their facing duration ( $P < 0.001$ ), than squirrels in the snake-selected group. They also spent significantly ( $P < 0.05$ ) more time within striking range of the gopher snake than the snake-selected squirrels. The two groups did not differ appreciably in the number of substrate-throwing acts and tail-flagging cycles, although individuals within both groups varied considerably in the expression of these behaviors.

Pearson product-moment correlations with Bonferroni probabilities were used for the entire sample of 80 squirrels to examine the consistency of antisnake behavior during encounters with the rattlesnake and gopher snake. All five behavioral measures were positively correlated at  $P < 0.001$ . Tail piloerection yielded the strongest correlation ( $r = 0.470$ ), followed by substrate throwing ( $r = 0.452$ ). Inspection of the scatter plots for tail piloerection (Fig. 2A) shows two overlapping distributions with different mean values, accounting for the high positive correlation. When examined separately, the correlations dropped to non-significant values (snake-selected group,  $r = 0.249$ ; relax-selected group,  $r = 0.293$ ). These changes illustrate the sensitivity of Pearson product-moment correlations to latent grouping in the distributions and, therefore, the value of examining each group separately (Meehl, 1973). Squirrels in each group were much more consistent in levels of substrate throwing (Fig. 2B), maintaining correlation coefficients closer to that of both groups combined (snake-selected

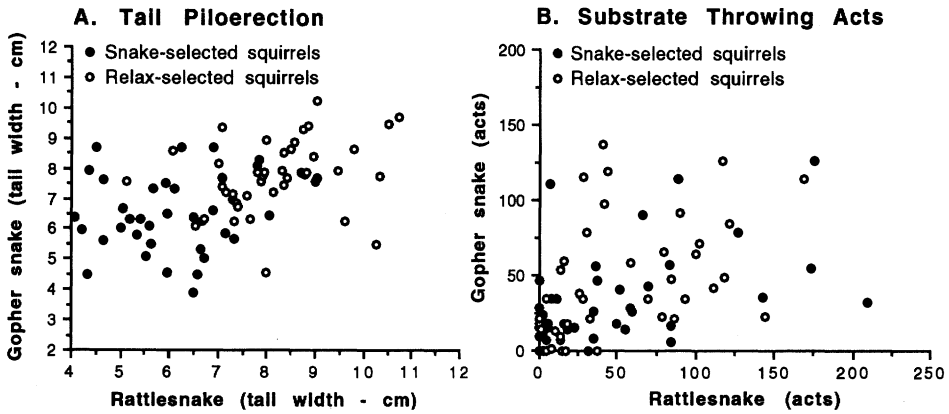


FIG. 2.—Scatter plots of tail piloerection (A) and substrate throwing (B) during trials with the rattlesnake and gopher snake. Note the distribution of the two clusters of snake-selected and relax-selected squirrels (A) that yield a significant positive correlation when pooled and a nonsignificant correlation when each group of squirrels is examined separately. The distributions of the two groups of squirrels for substrate throwing (B) are relatively similar.

group,  $r = 0.473$ ; relax-selected group,  $r = 0.444$ ). The multiple applications of substrate throwing outside the context of dealing with snakes might account for the similarities in these correlations.

*Canonical correlation analyses.*—The use of two different species of snakes allowed an assessment of differential treatment of venomous and non-venomous snakes by *S. beecheyi* (Coss et al., 1993; Towers and Coss, 1990). The use of populations currently sympatric or relatively allopatric with rattlesnakes and gopher snakes allowed an assessment of how this relationship changes with relaxed selection. The use of two arousing contexts for each individual allowed assessment of the role of temperament. Canonical correlation analysis was performed separately for the two groups of squirrels. The general goal of canonical correlation analysis is to describe the covariance matrix common to two sets of measures on a single individual by analyzing them as linear composites of observed variables (Darlington et al., 1973). The five behavioral measures from encounters with the rattlesnake comprised one set of variables, and their counterparts from encounters with the gopher snake comprised the other set.

Examination of the structure matrix after varimax rotation revealed important differences between the two groups in their treatment of the two snakes. The composite pairs related by significant canonical correlations (Bartlett's  $\chi^2$  approximation,  $P < 0.1$  for descriptive purposes) were composed of a much more complex structure in snake-selected *S. beecheyi* than in individuals from habitats where these snakes were rare or absent (compare Figs. 3 and 4).

Among *S. beecheyi* from locations with high densities of snakes the composites described by the first three canonical functions seemed to reflect traits that are involved in successful confrontation of predatory snakes (Fig. 3). The first correlation ( $r = 0.706$ ) reflected a correlation between monitoring the rattlesnake and signaling during encounters with the gopher snake. The second correlation ( $r = 0.607$ ) showed a relationship between aggressive confrontation of the gopher snake and tail flagging with the rattlesnake. A complement of the first correlation, the third correlation ( $r = 0.516$ ) reflected a correlation between displays of aggression toward the rattlesnake and monitoring the gopher snake.

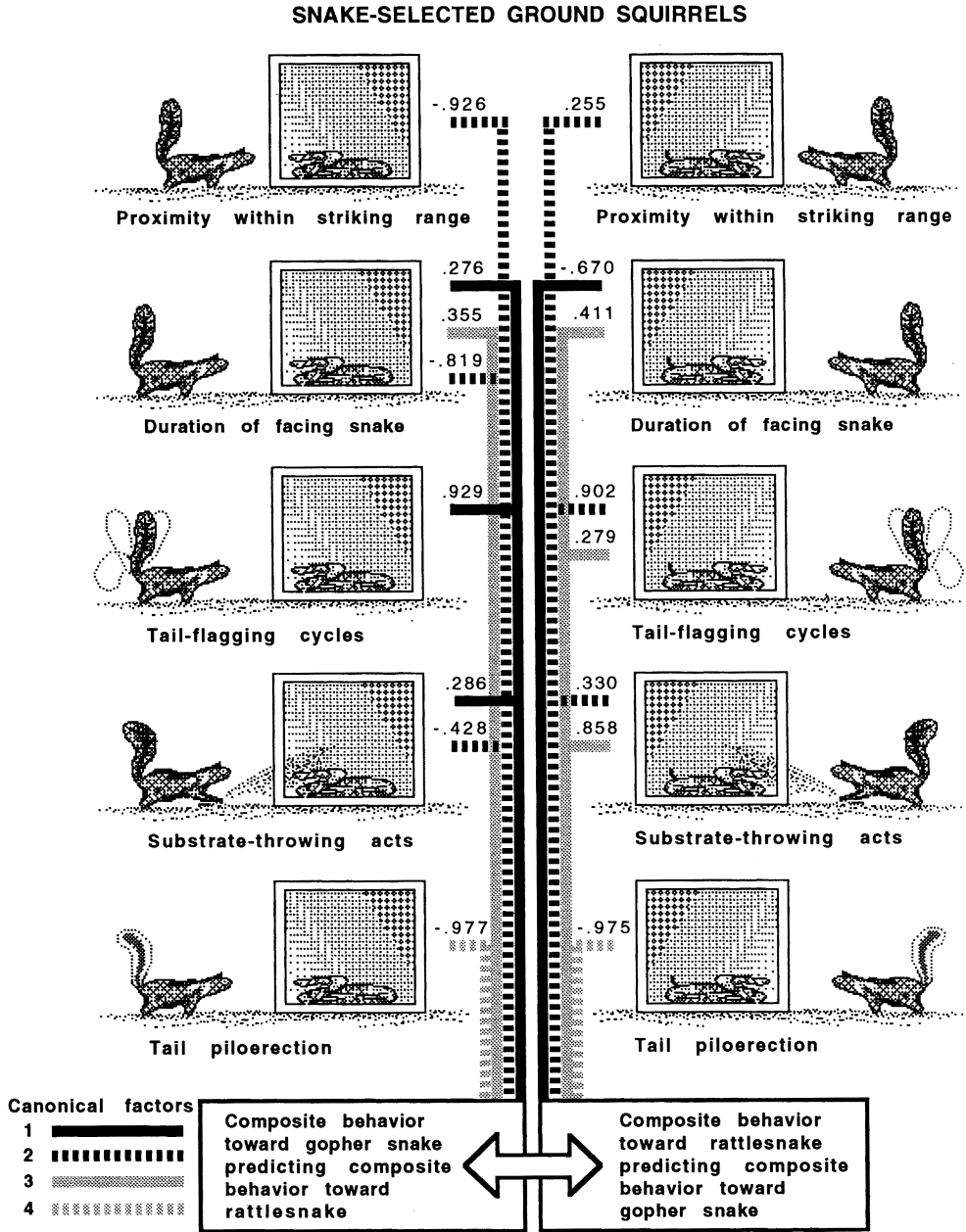


FIG. 3.—Factor structure of the first four canonical correlations for snake-selected ground squirrels during presentations of a rattlesnake or gopher snake. Inset numbers represent varimax-rotated weights, which are the correlations of the univariate measures with the composite antisnake behavior toward the gopher snake (left) and rattlesnake (right). Note that factor 4 is composed exclusively of the physiological arousal measure (tail piloerection), which does not contribute to the first three correlations.

RELAX-SELECTED GROUND SQUIRRELS

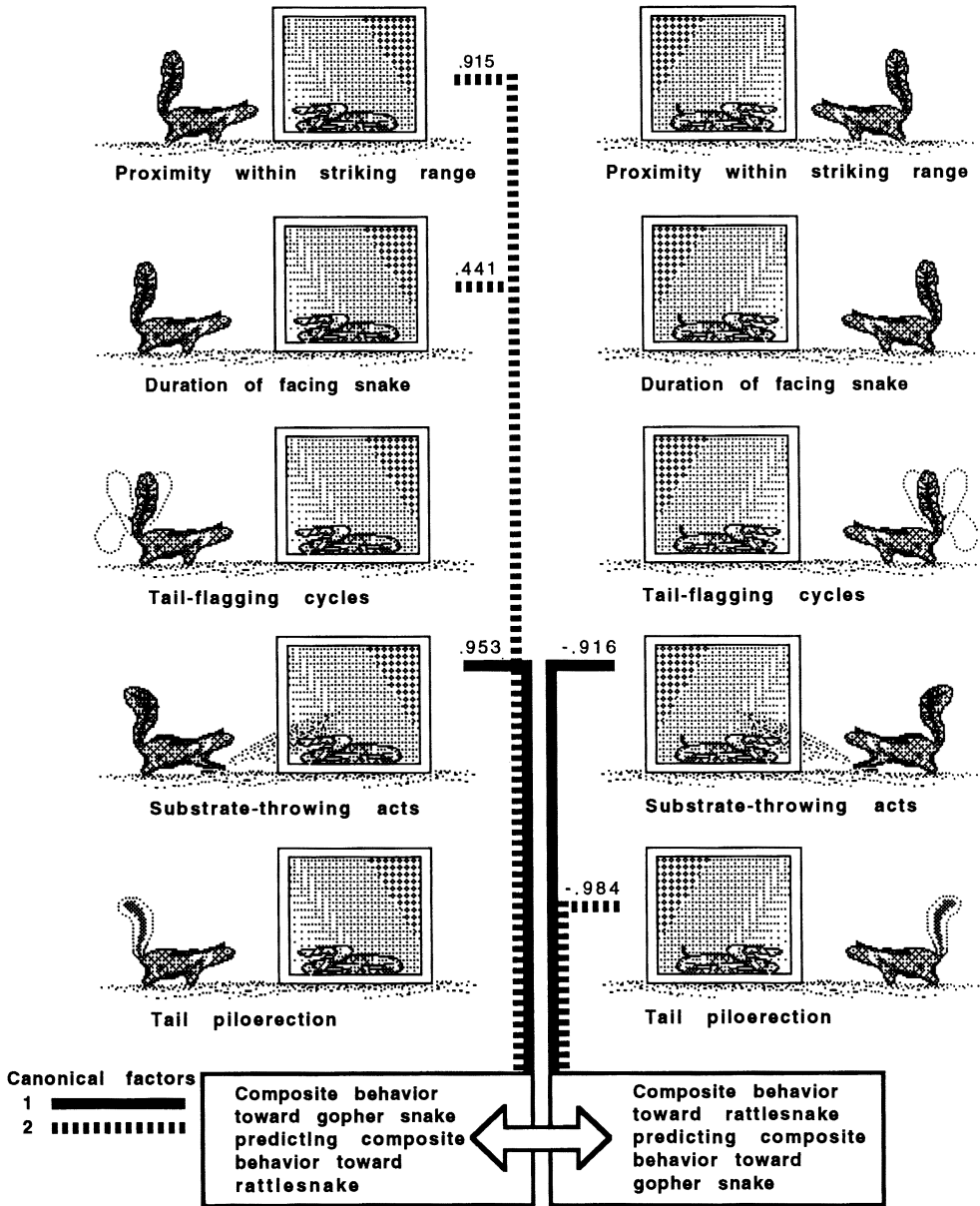


FIG. 4.—Factor structure of the first two canonical correlations for relax-selected ground squirrels during presentations of a rattlesnake or gopher snake. Inset numbers represent varimax-rotated weights. Compared with Fig. 3, the canonical composites have much simpler factor structure that might reflect disintegration of organized antisnake behavior with prolonged relaxed selection. In this group, tail piloerection is not isolated from investigative behavior (factor 2).

The final significant canonical correlation ( $r = 0.434$ ) is interesting in its own right. The composites incorporate only arousal toward the rattlesnake and gopher snake (Fig.

3). In fact, tail piloerection does not load on any other canonical composite and is decoupled from any of the other behaviors within and between species of snakes.

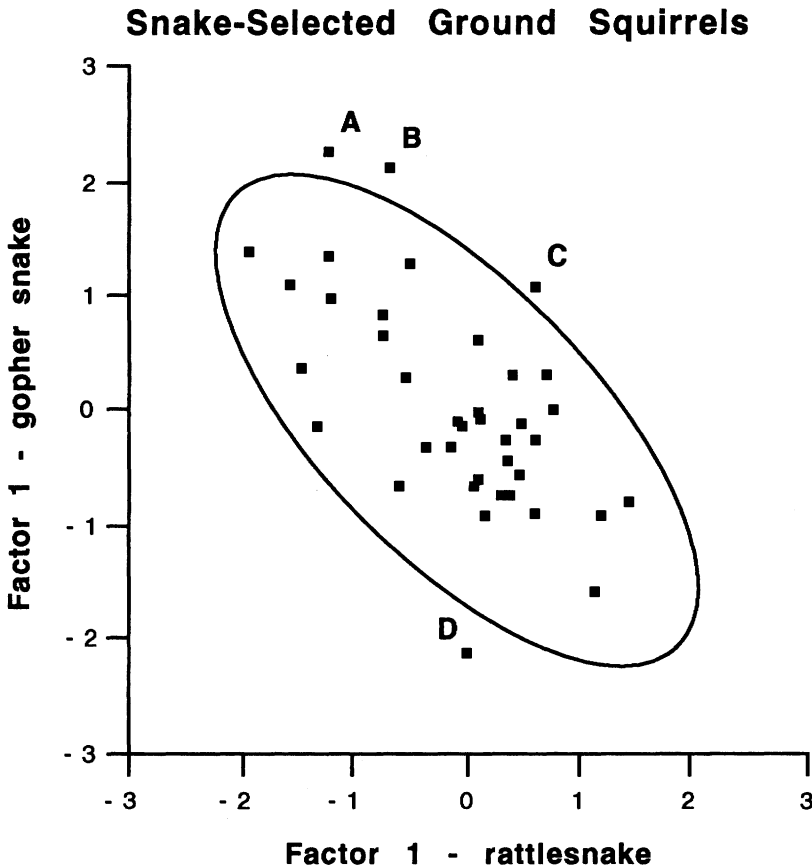


FIG. 5.—Scatter plot of ground squirrels from snake-abundant habitats in the first canonical correlation of behavioral composites. The ellipse encompasses 90% of the bivariate distribution. See text for behavioral descriptions of labeled outliers.

For *S. beecheyi* from locations where rattlesnakes and gopher snake were rare or absent, canonical correlation analysis presented different results. Most noticeably, the structures of canonical composites are much simpler (Fig. 4). In contrast to the snake-selected group, each of the five behavioral measures seemed to contribute only to a single canonical composite. The single canonical correlation that differed significantly from zero reflects this simplicity. The first canonical correlation ( $r = 0.689$ ) represented a correlation between substrate throwing toward the two species of snakes. High loadings of single measures simply restate the univariate Pearson product-moment correlation noted above for substrate throwing by relax-selected squirrels. The second correlation ( $r = 0.490$ ) was not

significant, but is presented in Fig. 4 to illustrate that physiological arousal was not decoupled from other confrontational behaviors as it was for snake-selected squirrels. Even in this case, the pattern is quite different from the snake-selected group, where the majority of composites reflected contributions from sets of two or more measures. On the whole, there appeared to be a lack of organized behavior employed by this group during encounters with snakes.

Variation in the composite measures characterizes uniqueness in the tactics used to confront snakes. The outliers in the first canonical correlation (Fig. 5) exemplify notable differences from the group averages and can be interpreted by returning to the univariate measures for these individuals (note that the weights shown in Figs. 3 and

4 are not the same as those used to calculate the composites; Thompson, 1984). For example, in Fig. 5, squirrel (A) faced and threw substrate at the rattlesnake at comparatively high levels while maintaining a low state of arousal. His low level of arousal with the gopher snake was still accompanied by average levels of these measures. Squirrel (B) also was aggressive toward the rattlesnake and maintained below-average arousal, but he was even more relaxed with the gopher snake, throwing substrate and tail flagging well below group averages. In contrast, squirrels (C) and (D) were highly aroused by both snakes, especially the rattlesnake, which they treated aggressively. However, squirrel (C) passively monitored the gopher snake without engaging in much harassment, while squirrel (D) treated the gopher snake more aggressively than group averages. The frenetic harassment of the rattlesnake by squirrel (D), which prompted striking and rattling, is particularly relevant when arguing that a high state of arousal might compromise the organization of appropriate antisnake behaviors. All four of these individuals exhibited distinctive antisnake behavior possibly modulated by temperament that selection may discriminate.

#### DISCUSSION

We examined variation in antisnake defenses at the level of individuals, litters, and selective regimes. Recognition of snakes as dangerous was apparent for all *S. beecheyi* studied, irrespective of age or current and historical contact with snakes as predators. Perception of danger in adults was identified by key behaviors, such as the rapid onset of tail piloerection, intense vigilance, pausing in elongate postures, and jumpiness. These behaviors are distinctly different from the investigative behavior of Arctic ground squirrels that fail to treat snakes as dangerous (Coss and Goldthwaite, 1995; Goldthwaite et al., 1990).

Recognition of snakes as predatory threats by all squirrels examined here also is evident in previously published descrip-

tions of 195 squirrels studied in the laboratory since 1975 (Coss, in press). Lack of individual variation in this trait is presumably the result of historical directional selection that has been sufficiently consistent to deplete the additive genetic variance (Mousseau and Roff, 1987). Mutation and recombination have not restored the additive genetic variance within the time period of relaxed selection acting on some populations of *S. beecheyi*. Additional constraints on mutational changes might involve perceptual processes used for recognition of snakes that also are shared by other perceptual systems still under selection (Coss, in press; Coss and Goldthwaite, 1995). Finally, a third source of buffering could involve the enormous pleiotropy in the way neural networks are constructed embryologically (Thaker and Kankel, 1992).

Although recognition of snakes can be accompanied by immediate defensive behaviors in an ambush situation, in other cases a slow-moving snake allows for the expression of long-term tactics that could manage its activities (Owings and Hennessy, 1984). As engendered by the experimental settings in both our studies, the progressive unfolding of antisnake behavior under less urgent conditions unveiled individual differences in the emotional and motivational states that modulated confrontational antisnake behavior.

In Study 1, developmental stability in the propensity to investigate the caged gopher snake and cat was not evident during the 2-week test interval. Low age correlations were the product of differences in litters when juveniles reversed their level of close investigation of the two predators as they aged. Strong positive correlations were apparent, however, for investigation of the two animals on the same day (Figs. 1E and 1F). With the exception of substrate throwing, comparisons of ages revealed the presence of short-term motivational states at specific ages that were not predictive of longer-term developmental outcomes.

Some facets of antisnake behavior with a

high degree of individual variation involve motor patterns, such as tail flagging, unique to dealing with snakes. In the lab, tail flagging is much less variable than as observed in nature (Hennessy et al., 1981; Hersek and Owings, 1993). Substrate throwing has much broader applicability, possibly to spur unidentified burrow intruders into species-specific actions (Goldthwaite et al., 1990; Towers and Coss, 1990). However, its variability is due, in part, to context as seen in Study 1 (Fig. 1C). The lack of cautious elongate postures during face inspection (Coss, 1993: figure 5) suggests that the cat was not recognized as a predatory threat, but was treated as a novel animal worth probing with substrate throwing.

In Study 2, examination of wild-caught squirrels from 10 sites distributed widely in California and Oregon permitted assessment of individual variation in the higher-order properties of antisnake behavior at the species level. Presentation of a rattlesnake and gopher snake in a balanced order separated by a 5-day interval provided the opportunity to examine short-term continuity of antisnake behavior and the effects of temperament. For *S. beecheyi* from sites where snakes were common, this allowed us to examine behavior currently subject to selection, while for sites where snakes were rare or absent, this context aided in assessing the disintegration of antisnake behavior. Canonical correlation analysis revealed changes under prolonged relaxed selection in the cohesive properties of action patterns. The structure matrices also illustrated that the two snakes were recognized and treated differently.

In snake-selected squirrels, the first three sets of canonical composites represent potentially adaptive composite groupings of vigilance, spacing, and confrontational behaviors. The fourth set reflects arousal of the sympathetic nervous system, completely decoupled from any of the other variables (Fig. 3). In contrast, tail piloerection of relax-selected squirrels when dealing with the rattlesnake is linked with

proximity and duration of facing the gopher snake (Fig. 4).

Populations of *S. beecheyi* sympatric with snakes as predators generally were less aroused physiologically than relax-selected squirrels (Fig. 2A). Differences in arousal engendered by the two snakes suggests strongly that the coupling of recognition of snakes and arousal of the sympathetic nervous system is relatively specialized. This situation-specific arousal would not be categorized as a temperamental trait. The coupling of arousal with measures of fearfulness in the relax-selected squirrels (Fig. 4) could reflect loss of arousal inhibition, permitting the reemergence of an ancestral condition in which squirrels presumably dealt with snakes under high states of arousal and fear. An elevated state of arousal while engaging snakes might compromise the success of such confrontations. Other studies have shown that sustained elevated arousal impairs memory processing in rats (Goldstein et al., 1994) and rapid decision making in humans (Shurtleff et al., 1994).

Previous research (Poran and Coss, 1990) describing developmental stability in the antisnake behavior of lab-born young of *S. beecheyi* tested 2-years later as adults focused on similarities in mean values rather than consistency in individual differences. The findings of the current study using correlational methods over much shorter time periods show that *S. beecheyi* exhibits considerable individual variation in behavior after recognition of snakes despite laboratory control of aversive consequences. It is still unclear how this variation interacts with the stochastic elements of encounters in natural settings.

Our evidence shows that physiological arousal in snake-selected squirrels is decoupled from the spatial and temporal patterning of antisnake behaviors and that level of fearfulness is intertwined with short-term motivational states. Together, these data provide clues into how temperamental influences on behavior might be minimized under threatening conditions. However, in-

dividual variation in aggressiveness revealed by substrate throwing appears to be a relatively stable component of temperament. Unlike the specialized aspect of investigating something snake-like, aggressive behavior can be used for dealing with adversaries in a variety of contexts unrelated to snakes; its prominence in relaxed-selected squirrels disassociated with other antisnake behaviors further emphasizes its temperamental properties. On the whole, higher-order stability in fitness-enhancing consequences might be sufficient to prompt the evolution of reliable higher-order properties of antisnake behavior useful for dealing with snakes in different microhabitats. Further study of interactions of ground squirrels with rattlesnakes and gopher snakes in the field and lab must attempt to specify the results of selection on higher levels of organization of antisnake behavior by evaluating their functional properties.

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