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DIFFERENTIAL TOXICITY AND TASTE AVERSION TO STRYCHNINE OF THREE SUBSPECIES OF THE CALIFORNIA GROUND SQUIRREL (*Spermophilus beecheyi*)

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ABSTRACT: Three subspecies of the California ground squirrel (Spermophilus beecheyi) were studied. In the first test of Experiment 1, Beechey (S. b. beecheyi), Douglas (S. b. douglasii), and, for comparative purposes, Sierra (S. b. sierrae) ground squirrels were each offered a drinking tube containing one of three H_20 solutions of strychnine sulfate (0.01, 0.05, or 0.5%) after being deprived of water for 23 hr. In Test 2 the survivors of Test 1 were offered for 24 hr a free choice of distilled water and two of the above concentrations of strychnine solutions. In Test 3 the survivors of Test 2 were offered for 24 hr a free choice of the same three concentrations of strychnine, but plain water was available. In the three tests, lethal amounts of strychnine solutions were consumed by 11 (79%) of the Douglas, none of the 14 Beechey, and 2 (18%) of the Sierra ground squirrels. In Experiment 2 the Douglas ground squirrels again proved to be the subspecies most susceptible to strychnine when compared with Beechey. In a third experiment, the squirrels did not reject strychnine bait on the basis of odor; however, in the fourth experiment Beechey ground squirrels that had been trained to reject strychnine-treated oat groats, a preferred grain, subsequently displayed much less interest in the olfactory cues from oat groats, suggesting that both previous experiences and olfactory cues are relied upon, at least in part, in their subsequent rejection of toxic food, even though strychnine sulfate may be odorless. These data help explain some of the problems associated with the use of strychnine as a rodenticide for the Beechey ground squirrel.

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INTRODUCTION

From an agricultural point of view, the two common economically important subspecies of the California ground squirrel, Beechey (Spermophilus b. beecheyi) and Douglas (S. b. douglasii), respond quite differently to strychnine-treated cereal baits (Clark 1986). When controlled as a pest, the Douglas ground squirrel can be poisoned with strychnine bait at any season of the year when the squirrels are active, whereas Beechey ground squirrels can be controlled successfully with strychnine only when they are consistently pouching large quantities of seeds in the fall, i.e., transporting them in their internal cheek pouches (Gabrielson 1932). When treated grain is pouched, the strychnine is absorbed through the mucous membranes of the cheek pouches (Pierce and Clegg 1915, Grinnell and Dixon 1918). It takes less strychnine to kill a ground squirrel when it is absorbed this way than when the bait is eaten (Dana 1962).

The laboratory phase of this study was conducted in the late 1960s to determine how these two subspecies differ in their acceptability, susceptibility, and learned aversion, both initially and subsequently, to strychnine. A third subspecies (S. b. sierrae) was used in several tests for comparative purposes. The results of this study have been used for a number of years to improve ground squirrel control strategy in California, although the study has not been previously published. Its value is in showing how subspecies of rodents can respond quite differently to a toxicant.

The main north-south demarcation of the geographical distribution of Beechey and Douglas ground squirrels is the San Francisco Bay and the Sacramento River, with the Douglas ground squirrel living north of the river (Hall and Kelson 1959). The Beechey and Douglas squirrels used in these studies were captured at locations several hundred miles apart to assure that the behavioral responses would be typical of the subspecies. The range of the more mountain-dwelling Sierra ground squirrel is not continuous with either of the other two subspecies and less is known of the response of this subspecies to strychnine as it is not considered a significant economic pest.

METHODS

The test animals consisted of 20 Beechey ground squirrels trapped near Santa Margarita, San Luis Obispo County; 19 Douglas ground squirrels caught near Davis, Yolo County; and 11 Sierra ground squirrels trapped near Blue Canyon, Placer County, California. All were adults, with both sexes represented. Strychnine sulfate, $(C_{21}H_{22}N_20_2)_2 \cdot H_2SO_4 \cdot 5H_20$, NF grade, was dissolved in distilled water to prepare the desired solutions. The solutions were formulated as though the sulfate was 100% pure strychnine.

The susceptibility of individual animals to given doses of strychnine in natural environments has been reported on occasion to be related to animal diet. Animals on diets high in tannic acid can consume larger doses of strychnine without fatalities (USDI 1967). To rule out any possible influence of previous diet on susceptibility, all animals were maintained on Purina mouse breeder chow for a minimum of 45 days before being tested.

Experiment 1

The three drinking tests with strychnine solutions were conducted in two-chambered cages. The home chamber (38x30x25 cm) was separated by a door from the test chamber (20x20x30 cm). Individual squirrels were normally confined to the home chamber and were permitted in the adjoining chamber, which was equipped with 1 to 3 calibrated drinking tubes when tests were under way. The cage and drinking assembly is identical to that described by Howard et al. (1968b) for similar studies with rats and pocket gophers.

The three subspecies of ground squirrels were each

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divided into three groups (Groups A through I) and acclimated to their individual two-chambered test cages for 6 days. Water consumption was measured during the last 4 days to ensure they were drinking normally and to establish baseline water intake. For the next 10 days of the test, the animals were isolated in the home chamber of their cages and daily deprived of water for approximately 23 hr, then allowed into the second chamber to drink plain water for 10 min. To ensure their daily water requirement was satisfied during this conditioning period, they were then allowed an additional 50 min to drink.

After this sequence was repeated for 10 consecutive days, the squirrels learned to consume much of their water requirement during the first 10 min in the test chamber. The mean daily 10-min intake of water during the last 4 days of this 10-day training period was established for each animal.

Test l.--On the day following completion of the training period, each of the 39 squirrels was offered for 10 min, following a 23-hr water deprivation, one drinking tube that contained one of three strychnine solutions (0.01, 0.05, or 0.5%), depending upon group designation. Immediately after the 10-min strychnine exposure, each animal was given untreated water ad libitum for a 24-hr period.

Test 2.--The following day, the 31 survivors of Test 1 were offered for 10 min a free choice of three drinking tubes of plain water and two strychnine sulfate solutions to determine whether an aversion had developed. Except for Group C (0.5%), one drinking tube contained the same strength of strychnine that the individuals had had in Test 1, plus one new concentration. In test 2 the squirrels were not deprived of water prior to its initiation and the test was for 24 hr instead of 10 min.

Test 3.--On the following day, the 29 surviving squirrels were each offered all three strychnine concentrations for 24 hr on a free-choice basis, with no plain water available.

<u>Experiment 2</u>

It has been documented (Gabrielson 1933) that the Beechey subspecies of ground squirrels are inherently more resistant to strychnine than are the Douglas subspecies. To confirm this, we gavaged four Douglas and nine Beechey ground squirrels of both sexes (from the same localities as those used in Experiment 1) with 5 mg/kg of strychnine sulfate solution. All individuals were observed continuously for 40 min and periodically for several days after being stomach-tubed. Unfortunately, no Sierra ground squirrels were available for this experiment.

<u>Experiment 3</u>

All of the Beechey and Douglas ground squirrels (Groups A-E) that survived Experiment 1 were placed one at a time in one of two body capacitor-olfactometer behavior arenas to monitor and record the number and duration of their food-seeking responses to the odors of the oat groats, with and without added strychnine sulfate.

The air flow olfactory device used was designed to monitor and record comparative responses of squirrels to olfactory cues (in an air stream) presented free of the influence of taste, without the reward of food, and without requiring any special laboratory training of these field-caught rodents. Basically, the olfactometer is a rectangular boxlike arena (1 ½ x 3 x ½ m). It has nine odor-emitting stations to accommodate three test odors, each replicated at three stations located in the floor of the arena beneath several inches of wood shavings. Each odor-emitting station contained an individual sensing unit (body capacitor) which monitors the presence of a squirrel if in the immediate vicinity. These olfactometer behavior devices have been described (with circuit diagram) by Zucker and Howard (1968) and Howard et al. (1968b, 1969).

Each animal was put one at a time in one of two olfactometers, where they were offered a choice of responding to the odor of oat groats that had been soaked in 3% strychnine sulfate solution, placebo oat groats that had been soaked in distilled water, and plain air. The two oat groat baits were prepared by placing 500 g of oat groats (with and without strychnine) overnight (15 hr) in 1 liter of water. The grain was removed the following morning and placed on shallow trays to air-dry. The two odors were produced by passing independent air streams over 25 g of placebo and treated oat groats, the test animal was deprived of food for 9 hr preceding the test. Just before the animal was released into the olfactometer arena (at 5 pm) from an enclosed nest box at one end of the arena, the sensory circuits and air flow were turned on to activate all nine odor-emitting stations. When the door from the nest box into the arena was opened, the laboratory was vacated by all personnel to avoid influencing the squirrel's behavior. The room lights were left on and the test terminated at 8 am, 15 hr later. With each subsequent squirrel, the odors were rotated in station position to compensate for any possible odor-station bias within the arena.

<u>Experiment 4</u>

This test was designed to determine whether olfactory cues were involved in subsequent refusal of strychnine-treated food by ground squirrels previously exposed to sublethal levels of strychnine offered on a selected food item. For this experiment, 10 new and naive Beechey squirrels (Group J) were selected. No Douglas ground squirrels were used in this experiment. Each squirrel was placed in the olfactometer and offered the choice of odors of plain air, oat groats soaked in 3% strychnine solution, and wheat soaked in distilled water. These were prepared in the same way as in the previous test.

After the 15-hr olfactometer test, each squirrel was then trained to refuse (shy from) strychnine-treated oat groats. This training was accomplished by offering them sublethal amounts of strychnine on oat groats. After 11 days of this exposure and the loss of 3 animals, the remaining 7 squirrels had learned to refuse all toxic kernels of oat groats offered and were considered for our purpose to be completely shy of strychnine-treated oat groats.

Each of these squirrels was then rerun in the olfactometer for 15 hr and offered a choice of odors of plain air, placebo oat groats, and "wheat" soaked in a 3% solution of strychnine. Thus, wheat, not groats, was treated with strychnine in these odor tests.

RESULTS

<u>Experiment 1</u>

Test l.--The less the concentration of strychnine, the greater was the amount of solution drunk by all three subspecies (Table 1). However, the greatest amount of strychnine consumed by almost every squirrel was from the 0.5% bottle, which is 10 and 50 times as concentrated as the other two solutions. An important factor is that all but one of the Douglas ground squirrels in Groups E and F consumed considerably more of the 0.05 and 0.5% concentration than did either of the other two subspecies, though still considerably less than normal water intake. All of Group F Douglas squirrels that were offered the 0.5% solution died, and one on 0.05% strychnine died the next day without consuming any strychnine in Test 2. A total of 6 of 14 (43%) of the Douglas and 2 of 11 (18%) of the Sierra ground squirrels consumed a lethal dose, whereas no Beechey squirrels died.

Test 2.--One Douglas ground squirrel consumed more strychnine solution (0.1%) than water (Table 2). Two of the remaining 8 Douglas ground squirrels (25%) took lethal amounts; several Beechey ground squirrels actually consumed more strychnine per mg/kg but did not die. If a dose that is normally lethal is consumed slowly over a 24-hr period, an animal may not be killed, as occurs with pocket gophers (Thomomvs spp.) (Lee et al. 1986).

Table 1. Mean individual daily intake of plain water prior to test and in Test 1 of three concentrations of strychnine sulfate during one 10-minute restricted drinking period.

Subspecies	Squirrel group (n)	Daily water intake ml (range)	Percent strychnine	Amount consumed ml (range)	Amount consumed mg/kg (range)	Number of deaths (%)
Beechey	A (5)		0.01	10.4 (3-28)	1.9 (0.5-5.9)	0
	B (5)	37.1 (24.8-49.4)	0.05	4.8 (2-7)	3.6 (2.5-4.9)	0
	C (4)		0.5	2.5 (1-4)	16.0 (8.5-20.0)	0
Douglas	D (5)		0.01	10.0 (3-21)	1.4 (0.3-3.6)	0
	E (5)	42.2 (37.2-49.9)	0.05	9.8 (5-22)	6.7 (3.3-18.7)	2(40)
	F (4)		0.05	6.0 (1-10)	44.5 (8.0-80.0)	4(100)
Sierra	G (3)		0.01	5.0 (3-8)	0.9 (0.7-1.3)	0
	H (4)	36.7 (34.2-39.3)	0.05	3.6 (1-5)	3.6 (1.1-5.3)	0
	I (4)		0.5	2.0 (1-3)	25.3 (11.5-43.5)	2(50)

Table 2. Mean individual intake in Test 2 by survivors of Table 1 of free choice of water and two strychnine sulfate solutions during a period of 24 hours.

Subspecies	Squirrel group (n)	Amount consumed, ml (range)				Combined amounts of strychnine consumed mg/kg (range)	Number of deaths (%)
		H_2O	0.01%	0.05%	0.5%		
Beechey	A (5)	37.2 (8-70)	5.0 (4-8)	--	3.0 (5-1)	29.2 (7.7-45.7)	0
	B (5)	16.2 (2-30)	--	3.0 (0-1)	0.6 (0-1)	5.9 (0.6-11.2)	0
	C (4)	13.3 (5-28)	5.0 (0-9)	3.0 (2-3)	--	2.9 (1.1-4.0)	0
Douglas	D (5)	10.6 (0-22)	18.8 (0-32)	5.0 (0.14)	--	6.3 (3.0-13.3)	1 (20)
	E (3)	43.3 (30-51)	--	2.7 (0.5)	0.0	1.8 (0.0-2.8)	1 (33)[b]
	F[a]	--	--	--	--	--	--
Sierra	G (3)	13.3 (3-22)	3.0 (1-6)	1.3 (1-2)	--	1.6 (0.9-2.2)	0
	H (4)	29.0 (6-59)	--	1.5 (1-2)	0.8 (0-1)	9.1 (3.7-13.2)	0
	I (2)	41.0 (30-52)	2.0 (0-4)	--	0.5 (0-1)	4.8 (2.9-6.7)	0

[a]All succumbed in Test 1.
[b]This animal died without consuming any strychnine in Test 2.

Test 3.--Three of the 6 remaining Douglas squirrels took a lethal dose during the 24-hr period (Table 3). They had consumed 1.5, 11.9, and 27.0 mg/kg of strychnine. The one that consumed only 1.5 mg/kg of strychnine probably died partly as a result of the strychnine consumed the previous day in Test 2. Some of the Sierra ground squirrels consumed the greatest amount of strychnine and survived.

Experiment 2

Three (75%) of the 4 Douglas ground squirrels died that were gavaged with 5 mg/kg (3.2-4.0 ml, depending on body weight) of strychnine sulfate solution. The fourth went into convulsions but survived. Of the 9 Beechey ground squirrels that received the same dose of 5 mg/kg (3.0-4.9 ml) of strychnine sulfate solution, only one (11%) died, one had convulsions, and two appeared sick but did not go into convulsions. Thus, 44% showed some overt effect, compared with 100% of the Douglas ground squirrels being affected.

Experiment 3

All of these squirrels had been exposed to strychnine on three previous occasions (Experiment 1, Tests 1-3), so they should shy from or be repelled by an odor produced by strychnine if the compound is not odorless to squirrels as it is to man (Stecher 1960). No significant preference was shown for odors coming from placebo oat groats over strychnine-treated oat groats, which suggests that strychnine provides no olfactory cues to squirrels. Beechey ground squirrels averaged 47.7% of their time (1537.5 sec) at the three strychnine-oat stations, 48.6% (1565.7 sec) at the tree placebo-oat stations, and 3.8% (121.4 sec) at the three air-only stations. The Douglas ground squirrels spent 54.8, 44.6, and 0.6% of their time at the same respective stations. In all of the olfactometer tests, the squirrels made many more visits and spent more time at the stations emitting odors of cereals than at those with just plain air, which is indicative of their preference for the food odors. Station visits of less than 15 sec were not recorded on the event recorder, but sometimes a squirrel spent as much as 25 min sniffing and digging at an odor-producing station.

Experiment 4

The 10 Beechey ground squirrels that were naive to the taste of strychnine and oat groats displayed a decided preference in the olfactometer for the odor of the strychnine-treated oat groats. They spent 80.6% of their time at the oat stations, 14.6% at the wheat stations, and 4.8% at stations emitting just plain air.

After they were trained not to eat strychnine-treated oat groats, they then spent only 46.5% of their time at the strychnine-oat groats station, 51.4% at the wheat, and 2.2% at the plain-air station. Before being conditioned to avoid strychnine-oats they spent 129.5 sec (14.6%) at the wheat station, but after being conditioned (i.e., averted) not to eat strychnine oats, the time spent at the wheat station increased to 2048.5 sec (51.4%), although wheat is a low-preference cereal with ground squirrels. Since they were hungry, their preference for wheat probably improved when the only other item available was oat groats. Apparently no strychnine odor was detected by the squirrels, but the previous experiences with sublethal ingestions of strychnine-oat groats resulted in the avoidance of the odor of oats, hence the carrier and not the toxicant provides the discriminating olfactory cue in this instance.

Table 3. Mean individual intake in Test 3 by survivors of Table 2 when offered a choice of all three concentrations of strychnine sulfate in absence of plain water during a period of 24 hours.

Subspecies	Squirrel group (n)	Amount consumed, ml (range)			Combined amounts of strychnine consumed mean mg/kg (range)	Number of deaths (%)
		0.01%	0.05%	0.5%		
Beechey	A (5)	1.2 (0-6)	1.8 (0-7)	0.4 (0-1)	5.1 (0.0-12.6)	0
	B (5)	0.8 (0-4)	0.4 (0-2)	0.0	0.1 (0.0-0.4)	0
	C (4)	3.3 (2-5)	1.3 (0-3)	0.0	1.5 (0.2-3.8)	0
		5.3	3.5	0.4		
Douglas	D (4)	8.5 (0-25)	2.8 (0-6)	2.8 (0-6)	9.5 (1.5-27.0)	2(50)
	E (2)	13.5 (0-27)	13.5 (10-17)	0.0	12.5 (11.9-13.1)	1(50)
	F[a]	--	--	--	--	--
Sierra	G (3)	23.7 (11-30)	3.3 (2-4)	1.3 (1-2)	23.1 (14.2-37.7)	0
	H (4)	24.3 (15-30)	2.3 (1-3)	0.8 (0-1)	12.4 (3.8-18.3)	0
	I (2)	19.0 (8-30)	0.5 (0-1)	0.0	6.0 (4.1-7.8)	0

[a]All succumbed in Test 1.

DISCUSSION

Of the three subspecies of S. beecheyi, the Douglas ground squirrels found solutions of strychnine sulfate considerably less objectionable upon their first two exposures than did the Beechey and Sierra ground squirrels. The Beecheys' aversion to strychnine is apparently so great that they will deprive themselves of fluids rather than accept even the lowest concentration, even though they could have consumed relatively large amounts of the lowest concentration without surpassing the lethal threshold. The differences were most apparent at the lowest concentration (0.01%). Aqueous solutions of strychnine sulfate taste very bitter and are quite objectionable to humans. The results of the first exposure of squirrels to strychnine solutions seem also to reflect some taste or palatability discrimination rather than more complex physiological reactions, since the availability of the solution was limited to a 10-min period.

Prien et al. (1963) reported that subconvulsant doses of strychnine sulfate had no effect on water intake when injected intraperitoneally prior to a 1-hr drinking period; therefore, we assume that strychnine intake, at least initially, does not diminish the thirst drive per se.

Douglas ground squirrels not only displayed less aversion to strychnine sulfate than did Beechey ground squirrels but were also more susceptible to strychnine. This is consistent with results reported for pocket gophers in comparison with roof and Norway rats (Rattus rattus and R. norvegjcus); the gophers also displayed less aversion to strychnine solution, yet were more susceptible to it (Howard et al. 1968b).

It has been suggested, in part on the basis of serum protein analyses by starch gel electrophoresis, that Beechey and Douglas ground squirrels are more distantly related than are the Sierra and Beechey (Marsh et al. 1969). We have no specific information on the susceptibility of Sierra squirrels; however, the number of fatalities suggests that they are somewhere between Douglas and Beechey.

Several factors in Tests 2 and 3 of Experiment 1 are not easily resolved: (1) Some squirrels may have been able to regulate their rate of intake of the aqueous solution of strychnine over the 24-hr period so that it was sufficiently physiologically detoxified or eliminated before it could poison them; (2) We had no way of measuring the lingering effects of strychnine from the previous day's intake; and (3) we know that induced tolerance to strychnine develops. Detoxification of strychnine in rodents has been reported (Crabtree 1962, Kalning 1968). Kalning showed no cumulation of strychnine or development of tolerance in mice, whereas others (USDI 1952) reported that such does occur at least in many species. Induced tolerance to strychnine by pocket gophers has been increased to where individuals have survived 12 days to 4 weeks when fed exclusively on diets of 1 to 1.5% strychnine-treated wheat (Howard et al. 1968b). This is further supported by Lee et al. (1990). Cooper and Krass (1963) suggest that the effects of strychnine may endure even if the compound is rapidly detoxified. They also suggest that the possibility of cumulative or sensitizing effects of repeated doses cannot be ruled out.

Observations indicate that zero toxic liquid consumption does not necessarily indicate that an animal did not taste the solution; it merely indicates that amounts were insufficient to measure. It is further likely that hyperlethal amounts of strychnine were taken in by many of the animals that succumbed.

The results of the first experiment with the olfactomcter suggest that squirrels are unable to detect strychnine by olfactory cues but can detect odor of food items. The ability of rodents to detect food by olfactory cues is well known, and a highly developed sense of smell has been demonstrated in deermice (Peromyscus maniculatus) (Howard and Cole 1967, Howard et al 1968a). Deermice have no difficulty locating even single buried seeds of conifers and cereals from olfactory cues, and many other rodents are presumably equally macrosmatic. Bull (1972), on the other hand, demonstrated with rats (R. norvegicus) that any initial attraction by odor must be reinforced by taste, and that odor plays a relatively minor role.

Shyness was directed primarily to the grain, but we cannot rule out the relationship of the oats and strychnine in combination as creating the necessary olfactory cue. The fact that the odor of oats was not avoided entirely in Experiment 4 by the squirrels that had been previously conditioned not to eat strychnine-treated oat groats, supports the fact that other cues, predominantly taste, play a major role in bait shyness. That rodents often develop shyness to toxic baits as a result of consuming sublethal amounts has frequently been demonstrated in rodent-control projects, but few have demonstrated the significance of odor in this shyness. In a previously published study (Marsh et al. 1970) using similar olfactometer techniques, we demonstrated that ground squirrels did use olfactory cues in discriminating against the rodenticide zinc phosphide once they became averted to that material.

Because of the preliminary nature and different objectives of our tests, there is no attempt to relate results with the behavioral studies of others who report that maze learning is facilitated by a low dose of strychnine (Lashley 1917, McGaugh and Petrinovich 1959, McGaugh 1961, McGaugh et al. 1962, Cooper and Krass 1963, Petrinovich 1963). McGaugh (ibid.) indicated that learning is disrupted by high doses, and Pearlman et al. (1961) correlated interference of memory or retrograde amnesia with convulsant agents.

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