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OLFACTION IN RODENT CONTROL

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ABSTRACT: A brief survey is presented of current knowledge on olfaction in rodents and the various roles that odors may play in modifying rodent behavior. Some species at least utilize olfactory cues: to locate food items; to recognize their mother and mates; to mark territory; as an involuntary population density regulator; possibly to recognize predators; as a warning cue against a repellent or toxic substance (poison-bait shyness); and probably, for many other behavioral purposes. The value of using artificial odors in rodent baits to increase bait acceptance is not yet well documented. The addition of attractive natural odors may increase detection of low-preference foods, but there is little evidence that a strange odor can improve palatability for any prolonged period. Much more research is needed before rodent control methodology can fully exploit the olfactory acuity of wild rodents.

A review is made here of knowledge on the role of smell in the ecology and behavior of wild rodents as it may relate to rodent control. Since so little is known about the role of smell and taste in the acceptance and rejection of baits by wild field and commensal rodents, it is hoped that this report will stimulate more research in this control area. Every rodent-control operator has his own theories about the significance of human odor on rat traps or the addition of a few drops of aniseed oil in a bait. Most of the evidence, however, is subjective. This paper discusses a number of aspects of olfaction and gustation in rodents which seem to bear directly on the role of odor in rodent control. Also reported are a few of our own preliminary findings.

According to Moulton (1967), the ability to detect, analyze, and exploit odors appears to reach its highest degree of development among mammals. Mammals are especially flexible and efficient in deploying their sensory resources and tend to make more use of all available cues. Many exploit odors extensively in trail-following, recognition of territory, of young, of mates, and of other social groups, as well as in the detection of food and predators. Furthermore, it is becoming increasingly evident that odors may control certain reproductive functions by acting as pheromones, as discussed later. Since the pairing of eyes and ears help an animal determine the direction of a stimulus, Moulton asks whether the pairing of the external nares, located so close together, serves a comparable function (tropotaxis). It could be, if very sensitive receptors could make simultaneous comparison of odor intensities or time of arrival. The high mobility of rodents and most mammals, however, may make this type of stationary orientation unnecessary. The volatile constituents of food actually in the mouth may also be smelled through intercommunication between olfactory and buccal cavities. According to Moulton (ibid.), Whitten observed that fluid from the mouth can travel up a cleft in the upper lip of the mouse to enter the nasal cavity. The snout of a mole is really a chemotactile sense organ, like the snout of a pig, where both tactile and olfactory information can be extracted simultaneously (Moulton, ibid.).

Mammalian chemoreception is associated primarily with taste buds or olfactory epithelium, and there appears to be no question that rodents have a highly effective olfactory modality, though little is known about the extent to which wild rodents use their olfactory senses to locate food items they may or may not have encountered previously. Research at Davis (Howard and Cole, 1967; Howard, Marsh, and Cole, 1968; Howard, Palmateer, and Marsh, 1969) has substantiated that at least in some wild rodents olfaction is high in the sensory hierarchy in richness of cognitive detail, in variety of sensory experience, and in motivational significance. Even so, research techniques must become much more sophisticated before we will know how to capitalize fully on the sense of smell of rodents in improving current rodent-control methods. Little is known about the extent to which various species of wild rodents use their olfactory senses to locate or avoid various food items; the significance, if any, of smell in affecting the palatability of foods to rodents; and how odor cues facilitate the locomotion, spatial orientation, and other ethological responses of rodents. It is generally known that the act of ingestion, normally a response to hunger, may be reinforced or inhibited by seemingly unrelated types of behavior and previous experiences. Some suspected or recognized factors include maternal instincts, social inter- and intraspecific stresses, population density and structure, hierarchy and dominance, tameness and fear, imitation and imprinting, general health and daily rhythm of the individual, season, temperature, and weather.

Our premise is that odor is what usually initially motivates a rodent to search for and pick up specific food items to satisfy its appetite, and that each rodent learns to associate its gustatory experiences with the odor of the item. Also rodents apparently have sufficient

memory that, through learning what is palatable and what is unpalatable, they base successful strategies for coping upon olfactory stimuli of the environment in which they live.

Since odor, especially in conjunction with taste, controls ingestive behavior of rodents to a large degree, we have made it the long-range goal in our Vertebrate Ecology and Institute of Ecology laboratories to determine the psycophysiological parameters of the olfactory cues that elicit the various orientation responses observed in different species of wild rodents. The types of ecobehavioral research undertaken or planned to measure the parameters include: determining the gross olfactory acuity of rodents for variously treated baits; isolating and characterizing (by gas chromatography, infrared spectra, etc.) the component volatile compounds which initially attract or repel various rodents; evaluating the olfactory relationships of the mechanisms (including genetic) responsible for producing bait and poison shyness; investigating the role of odor in the ability of adult rodents to communicate an awareness to their offspring, infant or weaned, that certain food items are unpalatable; measuring both the initial and the extended effects of odor per se on the palatability of foods; and determining the duration of conditioned shyness (associative memory) of rodents to the taste and smell of toxicants and bait materials.

The problems of technique are many in trying to get a wild rodent to respond at all naturally to odors and tastes. They need considerable space, thus necessitating outdoor pens, enclosures, or even field testing. Most wild species of rodents do not lend themselves to be trained for operant-conditioning tests, as is done so effectively with the laboratory rat, pigeons, and other domesticated species. The strength of odor used is important, for an otherwise attractive odor may sometimes become repellent if too intense, and the optimum strength to use is not easy to determine. It seems desirable to require the test subjects to exert some energy or work by forcing them to go out of their way in responding to the test substances. It is most important in olfactory studies not to provide the animals with something to eat when they seek out the source of an odor, for this would confuse gustatory preferences with olfaction. There is every likelihood, according to our results to date, that taste quickly dominates over odor once a test animal starts eating an odor-treated bait. The odor may serve as an attractant, but so far we have no indication that a new odor per se has any prolonged affect on the palatability of a food item.

Many types of olfactory devices have been used. We have developed a body capacitor-olfactometer chamber for quantitative measurement of the number and duration of odor-seeking responses of wild ground squirrels (Spermophilus spp.) and rats (Rattus spp.) to various olfactory cues presented free of the influence of taste, without the reward of food, and without requiring that the field-caught rodents first be trained to the olfactometer (Howard, Palmateer, and Marsh, 1969). The responses of the animals to the odor cues at the nine sensory stations in each test chamber are monitored by transistorized body capacitance relays (Zucker and Howard, 1968), which, admittedly, are not always easy to keep tuned. Six naive ground squirrels (Spermophilus beecheyi) were used individually in the olfactometer and exposed to the odor of oats (a highly preferred food) at three stations, to the odor of wheat at three, and to a flow of air from the animal room at the remaining three sensory stations. Before the airflow was activated, the total time out of 15 hours spent at the oat, wheat, and control stations, respectively averaged 0.5, 0.6, and 0.5 minutes. With an airflow at the flowmeter of 40 liters per minute the average total response times increased significantly (P < .005), respectively to 92, 15, and 5 minutes. It is interesting that the animals averaged a total of 1-1/2 hours at the sensory stations emitting the odor of oats, even though they were unable to feed on the oats (located elsewhere). The odors passed through 10 feet of glass tubing before reaching the sensory stations (Howard, Palmateer, and Marsh, ibid.). Responses were similar with wild Norway rats.

Other types of devices for measuring the olfactory responses of rodents include an apparatus to assess the reinforcing properties in small animals (Long and Tapp, 1968). In this instance the test cage is too confined for wild rodents. It does expose two odors, but each at only one location. The odors enter from the side of the cage and not from under a substrate, and the responses are monitored by lever pressing. Another apparatus, this one for audiorecording of animal sniffs (Teichner, 1966; Teichner et al., 1967) presents only one odor at a time since it is designed to measure olfactory thresholds. Also, in this equipment the rodent is forced into the test situation. A third type of olfactory device utilized a Y-maze, a rectangular box, and a circular choice apparatus consisting of an outer cylinder with drinking tubes projected inward, which rotates about an inner compartment (Eayrs and Moulton, 1960). In the Y-maze, rodents receive a positive reward (water) and observations have to be made visually. In the rectangular choice box the rat still receives a reward (water) and also receives a negative stimulus (shock) when an error is made. To keep the shocking grid exposed the floor cannot be covered. In the circular apparatus, observations are made visually and the odor sources are immediately available to the rodent

without requiring it to dig. Discriminations can be made only after a series of training periods for each rodent, and the rodent does not display any preference. Still another device uses the operant-conditioning procedure for studying olfactory discrimination (Pfaffmann et al., 1958). In this instance the rodent must press a bar when it smells the odorized air, and receives a positive reward for correct discrimination. French (1940) describes an olfactory-discrimination apparatus which requires visual observation of the rat's responses to different odors; however, the rodent receives a food particle, which in our opinion confuses palatability with olfaction.

Barnett and Spencer (1953) made one of the first studies of the attractiveness of the odor of aniseed oil and other smell and taste stimuli for wild rats. Even though aniseed had been so long and widely recommended as an attractant, they found that its smell was more of a deterrent. Nor was n-butyl nercaptan, peppermint oil, or butyric acid an attractant, but each of these three substances mixed with the wheat bait was a deterrent.

Interestingly enough, rats still regulate their food intake when taste, smell, touch, and other oropharyngeal sensations are completely eliminated. This was proven by delivering all food to a rat through a tube connected to its stomach by an automatic pump which was activated when the rat pressed a bar (Epstein and Teitelbaum, 1962). All test rats continued to ingest intragastrically (directly to the stomach via tubes) normal amounts of food offered in a liquid diet. They continued to digest a normal amount even when 0.05 percent quinine, normally a repellent substance, adulterated their diet. If the diet was diluted with water to half its concentration, they doubled their intake. They also maintained normal diurnal cycles during the tests. Obviously, then, the taste and smell of food and water, or the feel of it in the mouth, or proprioceptive feedback from the acts of oral eating and drinking "are not essential for the normal function of the central neural mechanisms regulating food and water intake in the adult rat" (Epstein and Teitelbaum, Ibid.).

Very little critical evaluation has been made of the effect of adding lures to rodent baits and traps. Rowley (1960) showed that raspberry essence, a rabbit lure used extensively in Australia, did not attract European rabbits to bait under field situations, in enclosures, or in pen conditions. The rabbits showed no preference between "lured" oats (containing the essence) and "unlured" oats. He concluded that smell plays but a small part in food-finding by the rabbit. This corresponds with observations by one of us (Howard) in 1957 in New Zealand from an automobile used as a blind. Rabbits located various food items placed in the field almost accidentally. They would go right past a small pile of oats, a carrot, or an apple, for instance, but should they happen to accidentally come upon one of these baits, then they would feed upon it. Both sight and smell seemed unimportant in their initial finding of these food items.

In recent years some very good work has been done on the effect of olfactory cues on the hormonal state of rodents. Pheromones are substances produced by some animals to induce one or more specific responses within members of the same species, e.g., the well-known air-borne sex attractants which are produced by the females of dogs and many insects. One of the best examples of pheromones operating with some rodents is known as the Whitten effect. Quoting from but one of his many references (Whitten, Bronson, and Greenstein, 1968), it has been demonstrated that male mice (Mus) produce a pheromone that, if transported by air movement to a group of female mice, not only will both induce and accelerate the attainment of estrous but will synchronize estrous among a significant proportion of females exposed simultaneously to the pheromone. The active substance, apparently a volatile odor in the urine of male mice, has not yet been identified. Other tests eliminated as causative factors all stimuli except smell.

The Whitten effect does not require the male to be present, for the females responded when placed in cages recently soiled by male mice (Whitten, 1956). Taste is not ruled out in this situation. Other tests have shown that urine from castrate males had no influence on the estrus cycle (Bruce, 1965), but that the pheromone was present in urine from normal males and urine from androgenized females with implants of 20 mg of testosterone (Bronson and Whitten, 1968).

An even more dramatic example of how olfactory stimuli can regulate sex hormones is the Bruce effect, wherein the presence of unfamiliar males immediately following coitus can cause pregnancy block, with the females returning to estrus (Bruce, 1960; Parkes and Bruce, 1961).

"In wild female house mice a skewed distribution of vaginal plugs on the days following pairing indicates an oestrus synchronization (Whitten effect) correlated with the presence of the male. Inseminated wild house mice were exposed to strange males or subjected to

various types of cage changes and handling during the preimplantation period. The strange males produced a significant reduction in pregnancy rates (Bruce effect). Changes in the physical environment produced comparable reductions in the absence of a strange male" (Chipman and Fox, 1966). Also, urine of a strange male rubbed on one of a pair of established males can elicit aggression between the formerly tolerant males (Archer, 1968).

The same type of pregnancy block has also been demonstrated in deer mice (Peromyscus) and Mus (Bronson, Eleftheriou, and Garick, 1964). But when soiled shavings from an over-population of deer mice (where reproduction function and maturation had been inhibited) were transferred to the pen of other deer mice, they achieved a higher (not lower) reproductive rate and generally larger reproductive organs than deer mice reared on unsoiled bedding or bedding soiled by bisexual pairs (Terman, 1968). Clearly much more information is needed about these pheromones. In the free-living laboratory populations of deer mice, various sociobiological factors (involuntary self-limitation of a population density) apparently were able to override the reproductively stimulating pheromones, even though surplus food and water were avilable, so that less than 10 percent of the females littered.

It has long been suspected that olfaction played an important role among many mammals in finding mates who were in heat. With rodents, LeMagnen (1953) showed that male rats used olfactory cues in choosing estrus females over diestrus females. Castrated and prepubertal males showed no preference unless injected with androgen. Carr and Caul (1962) showed that both normal and castrated rats could learn to discriminate by odor between estrus and diestrus females. They also found that both normal and ovariectomized females could discriminate between normal and castrated males. Thus, the hormonal state of the rat affects its preference for a mate, though not its ability to "discriminate" between the breeding condition of potential mates.

Any one who has housed laboratory mice (Mus) is acquainted with the obtrusive and unpleasant mousy smell of a colony. This smell comes from the secretion of the preputial glands in the males, and its purpose is to mark its territory or to establish dominance. Certain conditions will provoke this secretion. One is putting the mice into a clean cage, which males will then promptly mark. Thus, paradoxically, frequent cage cleaning may result in a "smellier" mouse room than one in which cages are cleaned only once in 2, 3, or 4 weeks (Lane-Petter, 1967).

Mating behavior in sexually naive and sexually experienced male golden hamsters (Mesocricetus auratus) was totally eliminated by removing their olfactory bulbs (Murphy and Schneider, 1970).

Whether individual recognition between rodents occurs in nature has not been determined; however, it has been shown that odor cues can be used by mice to discriminate between two males of the same inbred strain and between Mus and Peromyscus (Bowers and Alexander, 1967). Experiments designed to clarify the role of olfactory stimuli in sexual isolation between closely related and allopatric mice, Peromyscus maniculatus rufinus and P. polinonotus leucocephalus, revealed consistent responses oriented to the odors of their own species (Moore, 1965). Young gray squirrels (Sciurus carolinensis) have been shown to use both olfactory and visual stimuli in the "following" responses, which enables them to follow their mother (Hailman, 1960). It has been demonstrated (Hesterman and Mykytowycz, 1968) that both sexes of the European rabbit (Oryctolagus cuniculus) have as part of the rectum paired anal glands which secrete into the lumen of the alimentary canal at the junction of the anus and rectum. The size and secretory activity of these glands increase during the breeding season, being most pronounced in dominant males. The intensity of the odor is highest in the pellets passed by males to mark territories (Mykytowycz, 1968). The European rabbit has also been shown to use secretions from a chin (submandibular) gland for marking territories (Mykytowycz, 1966a) and secretions from the inguinal gland for sex-attracting (Mykytowycz, 1966b). The small depressions scratched out by rabbits, where urine and a few feces are deposited on the mound of soil, also probably provide an olfactory communication (Howard, 1958).

Deer mice (Peromyscus maniculatus), on the other hand, have been shown (Howard and Cole, 1967; Howard, Marsh, and Cole, 1968) to rely on olfactory stimuli, without visual cues, in detecting buried seeds. The propensity of this species of forest rodent to feed on Douglas fir and other conifer seeds has long plagued forest reseeding operations (Smith and Aldous, 1947; Spencer, 1954; Tevis, 1956; Dick et al., 1958; Hooven, 1958; Abbott, 1961). Seed losses from rodents and others (e.g., birds and invertebrates) often amount to 70 to 100 percent of the viable seed (Tevis, 1953; Boyer, 1964). There is great need for a means of making conifer seeds smell unattractive to deer mice and other forest rodents, and of being able to isolate

attractant odors which can be added to baits designed for forest rodent control. Baits with attractant odors would greatly reduce the total amount needed, thereby minimizing environmental contamination and ecological imbalances that otherwise might result.

In pen studies, when safflower oil was added to whole wheat, a low-preference food for deer mice, not only were more of the buried wheat kernels dug up but the number that mice carried away and presumably ate increased from 20.6 to 97.2 percent (Howard and Cole, 1967). The odor apparently increased detection, but increased palatability may well have reflected the palatability of the oil rather than odor attractiveness, as we assumed at that time. In subsequent tests (Howard, Marsh, and Cole, 1968), we confirmed that safflower oil or lecithin mineral oil improved detection and palatability with the four types of grains used. We are now more inclined to agree with Barnett (1963), who stated that it seems likely, although not proven, that odor leads to the first sampling by rats. He found that a wide range of odors seemed to induce licking, an activity usually followed by actual eating. Whether an attractive odor will lead a rodent to eat even a small amount of a food which is normally considered unpalatable has not really been demonstrated to our satisfaction.

It appears that the olfactory tour de force of deer mice may be responsible for a good many of their behavior patterns. In food preference tests, the preference ratings for different kinds of cereals and conifer seeds was essentially the same regardless of whether the animals were live-trapped in a locality where these food items were present, i.e., the food preferences in this instance appeared to be innate rather than learned.

Mathematical models and techniques of analysis of the diffusion processes of "olfactory-acting" pheromones were presented by Bossert and Wilson (1963).

DISCUSSION

It is clear that an attractive odor will increase the chance that most wild rodent species (if not all) will locate a bait carrying the odor. We have not yet confirmed that rodents can be readily conditioned to associate an exotic odor with a palatable but less odoriferous bait material. If baits can be prepared with attractant odors, it would reduce the number of baits needed, thereby minimizing environmental contamination and ecological imbalances that otherwise might be created by excessive use of rodenticides. That some kinds of rodents can readily learn to recognize the odor of baits containing a toxicant and rodenticides like zinc phosphide, once they have taken sublethal amounts of them, has been well demonstrated in our laboratory. Some rats, after being fed wheat with a toxicant on it, will starve before eating even clean wheat. We have also confirmed that deer mice, for instance can remember an unpleasant association with a toxic bait for many months. Yet little is known about how odor affects the discriminative appetite of a rodent. How to capitalize on a rodent's sense of smell to improve the efficacy of rodent control is a challenging field that is in need of much more critical research.

ACKNOWLEDGMENTS

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