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THE SEARCH FOR APPLICATIONS OF CHEMICAL SIGNALS IN WILDLIFE MANAGEMENT

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IMPORTANCE OF CHEMICAL SIGNALS TO WILDLIFE

Chemical signals play a vital role in the lives of many wildlife species. Several review articles (Bronson, 1971; Chael and Sprott, 1971; Ralls, 1971; Eisenberg and Kleiman, 1972; Estes, 1972; Mykytowycz, 1972) have described the diversity of chemical signals, their glandular or excretory origins, and their effects on behavior and reproduction in a variety of wild animals. Most often, chemical signals (pheromones) from conspecifics have been investigated. However, interspecific signals or allomones (Eisenberg and Kleiman, 1972) as well as odors and flavors of certain food items (Hansson, 1973; Rice and Church, 1974) and prey odors (Burghardt, 1970) have been studied and have been found to have survival and chemical signal value to many species.

Successful use of many identified and synthesized insect pheromones for managing populations and controlling damage to crops and forests suggests a large potential for use of chemical signals to managing wildlife. Unlike insects, however, the higher vertebrates do not automatically respond every time the appropriate chemical signal is presented. Factors such as previous experience (Stern, 1969, 1970; Carr *et al.*, 1970; Lydell and Doty, 1972), level of specific circulating hormones (Carr *et al.*, 1966; Doty, 1974; Price, 1975), and social dominance level (Krames *et al.*, 1969; Jones and Nowell, 1973) will often determine whether or not the appropriate response is made. The young, inexperienced animal has the genetic capability (Mayr, 1974) of using chemical signals, but its proficiency in using and responding to them is often shaped through subsequent social experience (Lott and Hopwood, 1972).

Even the social insects are capable of habituation to sex pheromones if the stimulus is presented too frequently (Shorey, 1974). In studying the responses of higher vertebrates to chemical signals, the problem of habituation can be compounded by a variety of other mechanisms. For example, in tests of food odor attractants with rodents, the animal's ingestion of a food will control its olfactory response to that specific food (LeMagnen, 1963; Larue. 1975).

This complexity of response is among the reasons why chemical signals have not been widely used in wildlife management. Almost no work has been done on the practical application of chemical signals for managing birds, and work with mammals has been limited to attempts at directly or indirectly reducing damage to man's livestock, crops, and other products. For a number of years, the U.S. Fish and Wildlife Service has been involved in research to develop and improve methods for safely and effectively reducing such damage by wildlife. The rest of this discussion will focus on the three major damage situations where chemical signals have been used for this purpose: coyote predation on livestock, deer and elk damage to trees, and rat damage to crops.

In these wildlife damage situations, chemical signals have been used or proposed for five different kinds of behavior modification: (1) to attract the animal to an area, place, or object (area attractant or lure); (2) to repel or frighten it from an area (area repellent); (3) to encourage it to eat a food (food attractant or bait enhancer); (4) to repel it from eating a food (food repellent); and (5) to disrupt its normal reproductive patterns. The types of chemical signals investigated for these purposes have been:

(1) signalling pheromones such as sex attractants; alarm, fear, or stress odors; and territorial marking pheromones;
(2) primer pheromones such as those associated with estrus cycling or pregnancy block effects;
(3) attractant food flavors;
(4) repellent or aversive food flavors; and
(5) allomones from attractive prey, avoided predators, or competitive sympatric species.

APPLICATIONS TO PREVENTING COYOTE PREDATION

Coyote Damage

Each year, millions of dollars worth of sheep and other livestock, are lost to coyotes throughout the western United States (Balser, 1974a, 1974b). In spite of man's many efforts to control sheep predation by reducing coyote numbers, the population continues

to expand and is increasing in some areas. The species is extremely adaptable and will probably continue to inflict severe economic losses unless more effective management tools are developed through research. One of the present research priorities is developing better area attractants. A plausible subject for future work is developing effective area repellents.

Area Attractants

Effective coyote attractants are needed for two purposes: monitoring relative abundance and increasing the number of animals reached by control measures. These are also the two main practical applications of insect pheromones (Tette, 1974).

Since 1972 a survey has been conducted each fall in an attempt to monitor the relative abundance of predators in the western states. Scent capsules are placed in circles of sifted dirt at intervals on transects; each such scent station is examined daily for tracks, and the number visited by coyotes is used as an index to their abundance in the area (Linhart, 1973). The lure that has been used in the scent capsules is air-inoculated fermented egg product, commercially manufactured mainly as an eye-gnat attractant, but found several years ago to attract coyotes to live traps. Since the natural fermented egg product is subject to batch-to-batch variations in odor quality and since its commercial formulation may be changed in the near future, we are currently developing a synthetic fermented egg (SFE) formulation to replace it. By using a combination of gas chromatography and mass spectrometry, we have so far identified over 70 compounds in the natural product. With the help of a human odor panel (Guadagni, 1968), whose members were selected by the criteria of Wittes and Turk (1968), specific concentrations of these compounds have been incorporated into a synthetic material that the panel could discriminate from the natural product less than 60% of the time. We chose the human odor panel technique because of inherent difficulties involved in evaluating many fermented egg fractions with coyotes even in pens. This human odor panel technique has been used to assess rabbit scent gland odor intensity (Hesterman and Mykytowycz, 1968) but this technique does have some limitations as pointed out by Dryden and Conaway (1967). For example, shrews respond to side gland odors that are undetectable by humans. No discrimination test or a test for similarity judgments have been made with the coyote since our main priority was to develop an SFE formulation equal to the natural fermented egg as a coyote attractant. Thus far, pen tests and preliminary field tests near Zapata, Texas, have indicated that the SFE is at least as attractive as the natural product.

The development of other good lures that are selective for coyotes should permit more reliable censusing (for example, to correlate local livestock losses with coyote activity), more effective use of control devices such as traps and the M-44 cyanide cartridge, and more effective delivery of control chemicals such as toxicants, chemosterilants, or aversive agents. Over the years, trappers and others engaged in operational field control have used a vast assortment of organic scents and homemade formulations to attract coyotes, but little has been done to test the effectiveness of these materials. We are currently planning field tests with some of the commonly used ingredients, including synthetic musks, essential oils, decomposing animal products, urine, and glandular secretions, to evaluate the behavioral responses these materials elicit.

One group of compounds that may warrant further investigation for formulating selective attractants for coyotes, and possibly for other mammals, is the volatile short-chain fatty acids. These compounds make up about 75% of the natural and synthetic fermented egg attractants. Coyotes are also attracted to a synthetic monkey pheromone preparation (Keverne and Michael, 1971; Curtis et al., 1971) containing a specific ratio of five of these acids (acetic, isobutyric, isovaleric, isocaproic, propionic). In the Texas field test, this preparation elicited somewhat fewer visits than the two fermented egg products but more pronounced behavioral responses (such as rolling and digging). Exactly why coyotes are attracted to different ratios of volatile short-chain fatty acids is unclear at present. However, these compounds apparently occur widely in mammalian signalling systems. For example, they have been identified in the anal glands of coyotes and dogs (Preti et al., 1976), red foxes (Albone and Fox, 1971), weasels and Indian mongooses (Gorman, 1976), and guinea pigs (Beruter et al., 1974), and in vaginal secretions of Rhesus monkeys (Curtis et al., 1971) and man (Michael et al., 1974). There is evidence that mongooses use individual differences in volatile fatty acid ratios as a code to identify each other (Gorman, 1976). Thus, coyotes may be attracted to certain fatty acid ratios out of curiosity and to investigate other, unidentified coyotes, or because these ratios mimic odor cues from competing predators or prey. Volatile fatty acids are also known to be the products of protein decomposition. Because coyotes frequently scavenge for food, some animals could be attracted to the short-chain fatty acid odor due to a resemblance to carrion odor. The question of why coyotes are attracted to different volatile fatty acid ratios needs to be examined closely to define future applications for this group of compounds.

Area Repellents

Although area attractants are currently the most important research priority, area repellents may have some potential for

controlling coyote predation on sheep. We know, for instance, from the work of Peters and Mech (1975) that dominant male wolves have a marked influence on the territorial boundaries of their packs. It would be somewhat surprising if coyotes did not show a similar respect for the territorial scent marks of dominant males. It is highly unlikely that the scent of dominant male coyote urine placed near a flock of sheep would lead to avoidance of this easily accessible and abundant prey item for any sustained period. However, on open range where the sheep are moved every few days to new grazing pastures pre-marking the acreage with active components in dominant male urine could perhaps have a temporary repellent influence, and could be used to protect sheep especially as the herd is moved into new grazing pasture across coyote trails and established territories. An important question in this context is whether there are certain chemical compounds only produced by dominant animals or whether the response of subordinate animals is conditioned through physical agonistic encounters.

Other odors of natural origin might also be considered as area repellents. Most odors that have been tested with coyotes have been selected from various classes of chemical stimuli or lachrymators used as dog repellents (Lehner et al., 1976). But dog repellent chemicals are often selected on the basis of human responses to irritating or objectionable odors. The canid nose, of course, may tolerate these and respond more strongly to odors of which we are unaware. For example, it is often said that wild mammals can detect human odor, and Taylor et al. (1974) found that captive Norway rats responded to it, but the active components in human scent were not identified. Natural prey species such as certain lizards, snakes, moles, shrews, skunks, and toads may have effective chemical predatory defense mechanisms (Bolles, 1970) that allow them to travel unmolested through the territories of predators. As far as I know, no one has ever attempted to isolate repellent aversive compounds from these species for use in predator control. Working against this concept, however, is the fact that coyotes are extremely adaptable and will accept a wide variety of food items (Sperry, 1941) including prey usually considered malodorous or distasteful.

Most species seem to have mechanisms to ensure species isolation and prevent hybridization. Moore (1965) and Doty (1973a, 1973b), for example, found that deer mice were tuned to the odors of their own species or strain and rejected others. Coyotes apparently will socially accept and readily interbreed with red wolves and domestic dogs (Gibson, 1974; Riley and McBride, 1975). However, they may be rejected or be repelled by odors from other canids such as grey wolves or foxes. Bears and large felids, such as the mountain lion, may also produce territorial marks that coyotes avoid. As with pheromones, however, the coyote's response to allomones from competitive predators or avoided prey has never been adequately explored.

APPLICATIONS TO PREVENTING DEER AND ELK BROWSING

Deer and Elk Damage

As with many forms of wildlife, deer and elk can provide recreational sport hunting, and aesthetic resources to the public. At the same time, however, deer and elk may do appreciable damage to Douglas-fir seedlings (Kverno, 1964) in the Pacific Northwest. When browsing becomes too severe, the seedlings grow too thin and mature much later. The Denver Wildlife Research Center and our Forest Animal Damage Field Station at Olympia, Washington, have been involved in the development of deer repellents for a number of years (Campbell and Bullard, 1972).

Food Repellents

Of 255 chemicals that have been screened for repellent activity with black-tailed deer, only 3 - a putrified fish preparation, fermented egg product, and an animal rendering material, Wilson blood meal - have shown reliable repellent effects. Their repellency probably relates to the natural tendency of ungulates to avoid decomposing plant and animal material as food. The putrified fish and natural fermented egg products have been used to repel black-tailed deer from developing Douglas-fir seedlings. Concentrations as low as 10 ppm of certain components within putrified fish have been shown to repel captive deer in pens (Campbell and Bullard, 1972). The synthetic fermented egg (SFE) product previously described, proved to be equally repellent as the natural product. Later in development, to improve the SFE repellent activity, we again used human odor panel testing techniques to develop seven enhanced SFE preparations. Classes of compounds found in the natural product such as esters, amines, aldehydes, short chain fatty acids, sulfur compounds, C_7-C_9 fatty acids, and fecal odors (skatol and indole) were added to SFE until the odor panel could barely detect the odor change. These same materials were then tested on pelletized Douglas-fir feed with captive deer and elk in Olympia, Washington. The results indicated that the sulfurous compounds added to SFE provided more repellency than the untreated SFE for both deer and elk. The enhanced SFE work should allow us to develop a more simplified formulation for controlled release of volatiles after the active fractions have been identified.

Another natural repellent product found in the Pacific Northwest is wild ginger (*Asarum caudatum*). This plant material is rarely, if ever, browsed by deer and elk. Campbell and Bullard (1972) report that ground ginger shows a high repellency when added in ground form to feed. Field tests have shown high repellency to deer when this

material is applied to Douglas-fir seedlings (Personal communication, D. L. Campbell). Whether the effect is from odorous oils or bitter-tasting compounds is still, however, unknown.

Black-tailed deer are repelled from food by application of conspecific metatarsal scent placed underneath their feeding bowls (Muller-Schwarze, 1971). Only 42.3% of the food from the treated bowl was eaten compared with 97.3% from the untreated bowl. The responses of deer to this scent are somewhat complicated inasmuch as visual stimuli such as erected tail and auditory stimuli such as hissing or foot stomping also accompany release of the metatarsal scent when deer are stressed. Rochelle et al. (1974) also evaluated black-tail deer metatarsal scent placed on Douglas-fir branches but found the repellency to be short term, and they subsequently discontinued their research on deer-alarm pheromones.

Muller-Schwarze (1972) has also explored the concept of feeding suppression with allomones from predators. Six hand-reared black-tailed deer would not feed from bowls scented with feces from coyotes or mountain lions. Fecal scents from other non-sympatric predators produced less suppression. It should be noted, however, that fecal odors in general (Campbell and Bullard, 1972) are repellent to deer. Whole body odors, or odors from various glands of predators have not yet been tested for repellency with deer or elk.

APPLICATION TO PREVENTING AGRICULTURAL RODENT DAMAGE

Agricultural Rodent Damage

If either food sources, water, or cover are removed from vacant buildings, there is generally no infestation problem (Chitty, 1954; Barnett, 1963) with commensal rodents. However, the rodent problems often found in agricultural regions, especially where there is damage to the growing crop before harvest, cannot be controlled so easily. Fortunately, in the mainland U. S., rodent populations seldom, if ever, reach levels where entire crops are destroyed. Isolated crop areas are affected by such species as the pine and meadow voles in the Northeast in fruit orchards (Byers, 1975), deer mice in the Northwest in newly seeded Douglas-fir plantations (Kverno, 1964), and the Polynesian rat (Rattus exulans) in Hawaiian sugar-cane plantations (Hood et al., 1970). In other parts of the world, especially true tropical regions, rats cause extensive damage to grain and vegetable crops. The traditional approach to management of agricultural rodents has been population reduction by means of toxic baits and trapping.

Sex Attractants

The application of toxic baits for rodent control will probably be the main control tool for the next decade. A great deal of effort has been expended on improving bait palatability, trying to overcome bait shyness and toxiphobia, and developing bait formulations for weatherability.

The application of sex attractant pheromones to the toxic baiting method is somewhat questionable. For example, male hamsters show both licking of vaginal secretion and olfactory attraction to this secretion (Murphy, 1973). It has recently been demonstrated (Zahorik and Johnston, 1976) that male hamsters can also be conditioned to avoid water flavored with vaginal secretion after injection of a sublethal toxicant. Olfaction is so important to this species that olfactory bulb ablation in males will eliminate mating (Murphy and Schneider, 1970). Even though olfaction plays such an important role in the reproduction of this species, vaginal secretion as a sex attractant did not retard development of toxiphobia or sub-lethal aversion, but instead, served as an avoidance signal. Thus, sex pheromones that have biological survival value can be used as avoidance cues when they are associated with sub-lethal toxicosis. Nevertheless, such a material could work better than expected if the rate of feeding is increased to the point where the rodent ingests a lethal dose before the sub-lethal aversion occurs.

In an attempt to evaluate certain sources of sex attractant pheromones in ricefield rats (*R. r. mindanensis*), we have evaluated the response of sexually experienced males to female *R. r. mindanensis* odors using an in-cage preference apparatus (Shumake and Bullard, unpublished). The odor source materials were preputial gland exudate, fresh urine, and vaginal lavage material. Each material was collected from female conspecifics at the four estrus stages as determined by the vaginal smear method. As shown in Table 1, only proestrus urine produced a reliable increase in time spent by male rats in the presence of odor as compared with deionized water. Essentially the same experiment was replicated with female rats, but this time hair samples from the base of the males' tails were used in place of the vaginal wash. The females were tested this time as they cycled through various estrus stages; no statistically significant preferences were evident.

The proestrus female urine odor was the only material showing a reliable effect in the male rats, therefore we attempted to determine its effect on a normally poorly accepted bait. Using quinine levels (Shumake, Thompson, and Caudill, 1971) known to be rejected by wild Norway rats, we found that the proestrus urine produced no more effectiveness than tap water.

TABLE 1. ELAPSED TIME RESPONSE (SECONDS) OF MALE RICEFIELD RATS EXPOSED TO FEMALE ODORS (MEAN ± SE)

Stage of estrus of female sample	n	Odor source			
		Preputial gland	Urine	Vaginal wash	Water (control)
Diestrus	20	19.8 ± 6.5	10.6 ± 4.7	9.2 ± 3.0	23.7 ± 8.1
Proestrus	20	19.3 ± 8.4	100.5 ± 80.9*	49.5 ± 43.4	13.2 ± 8.1
Estrus	20	12.2 ± 3.2	59.5 ± 44.3	24.5 ± 10.1	29.9 ± 13.7
Metestrus	20	30.7 ± 11.8	7.6 ± 2.3	18.2 ± 5.9	7.5 ± 3.1

* P (test sample > water control) = 0.05.

Attractant Signals from Familiar and Preferred Food

Lacking information regarding other potential sources of pheromones in ricefield rats, we turned our efforts toward developing a highly palatable food flavor for rice bait for control of this species. Since rice, when it is available, is the most common food item found in ricefield rat stomachs (Tigner, 1972), we reasoned that this highly preferred and familiar food could be made more attractive to the rats in the field by the addition of certain naturally occurring rice flavor components.

A preliminary test with eight materials representing different components of rice grain (Bullard and Shumake, 1976) was run. Rice bran oil, ether extract of rice, endosperm, rice polish, bran, rice bran volatiles, and rice volatiles were all evaluated on groups of rats with a brief exposure taste preference device previously described (Thompson and Grant, 1971; Thompson et al., 1972). Only the rice volatiles material proved to be superior to untreated rice in many replications of the original preference test and in overnight individual animal preference tests. Results of a semi-natural test, shown in Table 2, confirmed the extent of this preference when whole grain rice, granulated rice, rice treated with 1% soybean oil, and rice treated with rice volatiles were used as bait bases.

As a final test of the toxic bait enhancing properties of the rice volatiles material (Bullard and Shumake, 1976), two groups of

TABLE 2. GRAMS OF RICE BAIT CONSUMED BY FIVE RICEFIELD RATS EACH IN FOUR ENCLOSURES (MEAN ± SE)

	Bait			
Day	(A) Whole grain rice	(B) Granulated whole grain rice	(C) Granulated whole grain rice treated with 1.0% soybean oil	(D) Granulated whole grain rice treated with trapped rice volatiles
1	8.1 ± 1.7	12.9 ± 2.7	22.8 ± 2.9	35.1 ± 3.2**
2	6.6 ± 2.1	8.9 ± 1.6	21.9 ± 2.3	35.1 ± 3.2*
3	5.3 ± 2.0	15.5 ± 2.7	25.9 ± 2.5	35.9 ± 3.3**
4	6.4 ± 2.4	14.6 ± 2.9	16.4 ± 3.0	34.4 ± 2.8**
5	5.8 ± 2.0	12.0 ± 2.3	19.8 ± 3.0	34.6 ± 2.6**
6	4.5 ± 1.7	15.6 ± 2.6	21.6 ± 2.6	36.8 ± 3.1***
7	5.5 ± 2.6	18.9 ± 2.4	15.0 ± 2.2	35.8 ± 2.7**
8	7.0 ± 2.8	19.1 ± 3.3	21.9 ± 3.0	32.4 ± 1.7**

* P(D>A)<0.10
** P(D>A)<0.05
*** P(D>A)<0.01

ricefield rats were offered two food cups for 7 hours per day for 3 days; one contained only the control formulation of untreated ground rice and the other cup contained this bait treated with 0.2% zinc phosphide, a commonly used acute rodenticide. The bait carriers were the control formulation for one group of rats and the rice volatiles formulation for the other group. There was much greater zinc phosphide dosage in the rice volatiles group (mean 33.9 mg/kg/rat/day versus 19.8 mg/kg/rat/day) and significantly greater mortality in the rice volatiles bait carrier group (14 dead versus 8 dead) after a 14 day mortality follow-up.

The advantage to working with flavors (both odor and taste stimuli) associated with a preferred food base is that rats eat the food base more rapidly when the flavors are intensified. Since the rice flavor is highly familiar to ricefield rats, toxiphobia to the bait base per se is reduced.

To improve the rice flavor additive quality to an even greater degree, we have also evaluated rice variety preference in R. r. mindanensis in order to extract volatiles from the most preferred varieties. The rats show a consistent preference ($P < .01$) for one particular variety, FK-178A, that has been commonly grown in the Philippines. IR-20 and C-4 were less preferred ($P < .05$) to FK-178A and Milagrosa. All four varieties, however, were preferred ($P < .01$) to the domestic California Brown Pearl (C.B.P.) rice. These same preference patterns were shown in both live-trapped adult animals and in laboratory born and reared ricefield rats. The preference pattern for certain varieties as shown by the live-trapped rats was much more distinctive, although similar, to the pattern shown by laboratory-reared rats.

Rice volatiles materials from FK-178A rice were compared with the volatiles from our standard California Brown Pearl rice in a later test to verify that rice flavor was the critical factor controlling the preference responses. Mean preference for FK-178A flavored rice was 64.3% compared with mean preference of 58.5% for C.B.P. flavored rice. This difference, although small, was reliable indicating that the rice variety preference data reflect primarily a flavor variable rather than texture, grain size, or nutritional level. Thus, volatile rice flavor materials collected from FK-178A should produce an even greater effect on zinc phosphide bait consumption than was shown with the C.B.P. rice flavor.

Signals to Disrupt Reproductive Patterns

The mode of action of certain primer pheromones is at present still somewhat debatable. The early work into this area (Bruce, 1959, 1960, 1961; Parkes and Bruce, 1961) implied that the odor of strange male mouse urine had the direct effect of blocking pregnancy. The evidence for direct pharmacological action of this foreign male odor is not supported by the fact that direct injections of strange male urine into pregnant female mice does not produce this effect (Mykytowycz, 1970). An alternate explanation may lie in the signalling function of the strange male odor. That is, the pregnant female is stressed by the strange male odor, and perhaps, innately recognizes the danger of carrying to term. Parkes and Bruce (1961) imply such a mechanism in their work. That is, if the stud male is of her own strain, then males of another strain are alien and block her pregnancy. However, if she first mates with a male of a foreign

strain, then males of her own strain are "alien" and pregnancy is again blocked.

In attempting to apply this pregnancy-blocking effect to population reduction of rodent species, we must deal with a complexity of problems. First, pregnancy is only blocked in 70-80% of the females. Kennelly et al. (1972) found that sterilizing 80% of male Norway rats had a negligible effect on a population over a 3-month period. One should expect birth control measures applied to female rodents to have a much greater effect on the population than male sterilization. However, their polygamous nature and capability of producing up to 8 - 10 litters per year can also work against female chemosterilant concepts. Second, the matter is somewhat further complicated by data (Lott and Hopwood, 1972) that indicate an experience factor in the olfactory pregnancy-block effect. Female mice (Mus musculus) are apparently sensitized to the alien male odor only if given sufficent sexual experience with a given male. It would thus appear that the pregnancy-block effect is extremely difficult to apply as a practical reproduction suppressor in the control of rodents.

Application of other primer pheromone effects such as the suppression of estrus cycling in mice (Whitten, 1959; Chipman and Fox, 1966) in the absence of male urine odor or the development of pseudo-pregnancies (Lee and Boot, 1956) are also difficult in operational terms. Such an application might involve the development of interfering odor materials that would not permit the females to perceive male urine odors existing in the ecosystem. Large-scale field application of such a material, however, would probably present many logistical and economical problems.

The feasibility of controlling rodents by confusing males with area-wide perfusion of female sex odors also appears to be extremely remote. Rodents do not rely exclusively on olfactory cues for mate seeking, courtship, or copulatory behavior. In general, olfactory bulb ablation has only minor influence (Johnston 1970, 1974; Bermant and Taylor, 1969) on the sexual behavior of male laboratory rats.

Area Repellents

Perhaps the greatest potential use of rodent pheromones lies in alarm, fear, or aggression-producing odors. When the predator population is high, perhaps the natural response of rodents to predator odors induces stress and produces a natural rodent population decline. Alarm pheromones from rodents or allomones from predators could have a dispersal effect on rodent populations. Stevens and Saplikoski (1973) have reported evidence of an alarm substance that is present in the blood and muscle tissue from conspecific rats. Hornbuckle

and Beall (1974) have confirmed these results. Fulk (1972) reported that voles tend to avoid places frequented by short-tailed shrews, an occasional predator. The odor source was apparently from shrew droppings.

To systematically assess the potential of alarm or stressor produced pheromones in rodents will probably require the comparative approach. The Polynesian rat (Rattus exulans) would be an excellent candidate species for evaluation of the dominant male stressor pheromone concept. Wirtz (1973) reported that the Polynesian rat has never been studied in its social context to any extent. Their midventral sebaceous glands as described by Quay and Tomich (1963) appear to be homologous to those found in gerbils (Thiessen et al., 1971). The report of Thiessen and Dawber (1972) indicated that Mongolian gerbils, a desert species, will attempt to cross water and many will drown rather than encroach upon territory marked out by dominant males. A behavioral method for bioassaying ventral scent gland secretion of the gerbil has also been published (Thiessen et al., 1974) and the active fraction was identified as phenylacetic acid. If the same dominant male scent gland marks exert as much influence on polynesian rats as in the gerbil or hamster (Johnston, 1975), it may be possible to protect Hawaiian sugarcane plantations with a synthesized dominant male odor. The concept would be even more promising if, for example, habituation effects could be delineated and defined in gerbils. The question here again is, will dominant male odor per se act as a durable barrier over a period of months or years? There are risks in expecting a repellent to continue working in the absence of further reinforcement, but other authors (Bolles, 1970; Hinde and Stevenson-Hinde, 1973; Muller-Schwarze, 1974) indicate that innate responses to naturally dangerous olfactory signals should not habituate, nor should they require learning experiences. Our work on odor attractants (Bullard and Shumake, 1976) indicates that odors and taste stimuli that occur naturally in the ecosystem have much more durable effects than those selected from non-biological origins.

SUMMARY OF CHEMICAL SIGNAL APPLICATIONS TO WILDLIFE MANAGEMENT

In the course of attempting to apply chemical signals to the management of certain wildlife species, we have tentatively developed the following guidelines:

(1) attractive odors and tastes have to originate from or be related to products that occur naturally in the ecosystem of the species to achieve success;

(2) odors that have specific communication content in one context (i.e., genital fluid ingestion for sex pheromones) do not necessarily lead to applications in another context (i.e., toxic bait consumption enhancement);

(3) repellent or stress provoking odors (signalling pheromones) may have as much or more application to wildlife management than the attractant pheromones;

(4) certain short chain fatty acids (i.e., the end-products of the action of bacteria upon protein breakdown products) are found in various ratios across diversified species and may form a chemical coding system for inter- and intra-specific signals; and

(5) other long chain fatty acids (e.g., oleic, linoleic, and stearic) are found in both plant and animal tissue and are probably the end-products of fat breakdown. These materials also appear to have attractant function for several species when added to a food source (Hansson, 1973).

Chemical signals form an integral part of the life of many wildlife species. The sources of these signals are not only from conspecifics but are also related to food items (prey and plant material), and possibly to the avoidance of competitive (Doty, 1973a) or predatory species (Müller-Schwarze, 1972). The stress provoking and dispersal capabilities of alarm or fear pheromones (Stevens and Saplikoski, 1973; Müller-Schwarze, 1974) in rodents and predators should be evaluated. Various means of delivering controlled dosages of chemical control agents (chemosterilants, toxicants, and aversive agents) under natural field conditions should be further explored in order to attempt application with attractant pheromones. The primer pheromone application to wildlife management presents extreme difficulty. Most mammalian species do not depend upon odor alone for mate detection and selection. Finally, although we are beginning to understand the importance of chemical signals as they affect the behavioral ecology of many wildlife species, a great many basic and comparative studies must be undertaken before field applications can be attempted.

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REFERENCES

Albone, E. S., and Fox, M. W. 1971. Anal gland of the red fox. Nature 233:569-570.

Balser, D. S. 1974a. A review of coyote control research. Proc. Sixth Vert. Pest. Conf. 6:171-177.

Balser, D. S. 1974b. An overview of predator-livestock problems with emphasis on livestock losses. Trans. North Am. Wildl. Nat. Resour. Conf. 39:292-300.

Barnett, S. A. 1963. The Rat: A Study in Behavior. Aldine, Chicago.

Bermant, G., and Taylor, L. 1969. Interactive effects of experience and olfactory bulb lesions in male rat copulation. Physiol. Behav. 4:13-17.

Berüter, J., Beauchamp, G. K., and Muetterties, E. L. 1974. Mammalian chemical communication: perineal gland secretion of the guinea pig. Physiol. Zool. 47:130-136.

Bolles, R. C. 1970. Species specific defense reactions and avoidance learning. Psychol. Rev. 77:32-48.

Bronson, F. H. 1970. General discussion (chapters 8-12), pp. 385-404, in J. W. Johnston, Jr., D. G. Moulton, and A. Turk (eds.), Communication by Chemical Signals, Vol. I. Appleton-Century-Crofts, New York.

Bronson, F. H. 1971. Rodent pheromones. Biol. Reprod. 4:344-357.

Bruce, H. M. 1959. An exteroceptive block to pregnancy in the mouse. Nature 184:105.

Bruce, H. M. 1960. A block to pregnancy in the mouse caused by proximity to strange males. J. Reprod. Fert. 2:138-142.

Bruce, H. M. 1961. Time relations in the pregnancy in the mouse caused by proximity to strange males. J. Reprod. Fert. 1:96-103.

Bullard, R. W., and Shumake, S. A. 1976. Food base flavor additive improves bait acceptance by ricefield rats. J. Wildl. Manage. (in press).

Burghardt, G. M. 1970. Chemical perception in reptiles, pp. 241-308, in J. W. Johnston, Jr., D. G. Moulton, and A. Turk (eds.), Communication by Chemical Signals, Vol. I. Appleton-Century-Crofts, New York.

Byers, R. E. 1976. New compound (RH787) for use in control of orchard voles. J. Wildl. Manage. 40:169-171.

Campbell, D. L., and Bullard, R. W. 1972. A preference testing system for evaluating repellents for black-tailed deer. Proc. Fifth Vert. Pest. Conf. 5:56-63.

Carr, W. J., Loeb, L. S., and Wylie, N. R. 1966. Response to feminine odors in normal and castrated male rats. J. Comp. Physiol. Psychol. 62:336-338.

Carr, W. J., Krames, L., and Castanzo, D. J. 1970. Previous sexual experience and olfactory preference for novel versus original sex partners in rats. J. Comp. Physiol. Psychol. 71:216-222.

Chael, M. L., and Sprott, R. L. 1971. Social olfaction: a review of the role of olfaction in a variety of animal behaviors. Psychol. Rep. 29:195-243.

Chipman, R. K., and Fox, K. A. 1966. Oestrus synchronization and pregnancy blocking in wild house mice (Mus musculus). J. Reprod. Fert. 12:233-236.

Chitty, D. 1954. The study of the brown rat and its control by poison. pp. 160-305, in D. Chitty (ed.), Control of Rats and Mice. Oxford, London.

Curtis, R. F., Ballentine, J. A., Keverne, E. B., Bonsall, R. W., and Michael, R. P. 1971. Identification of primate sexual pheromones and the properties of synthetic attractants. Nature 232:396-398.

Doty, R. L. 1973a. Odor preferences of female Peromyscus maniculatus bairdi for male mouse odors of P. m. bairdi and P. leucopus noveboracensis as a function of estrus state. J. Comp. Physiol. Psychol. 81:191-197.

Doty, R. L. 1973b. Reactions of deer mice (Peromyscus maniculatus) and white-footed mice (Peromyscus leucopus) to homospecific and heterospecific urine odors. J. Comp. Physiol. Psychol. 84:296-303.

Dryden, G. L., and Conaway, C. H. 1967. The origin and hormonal control of scent production in Suncus murinus. J. Mammal. 48:420-428.

Eisenberg, J. F., and Kleiman, D. G. 1972. Olfactory communication in mammals. Annu. Rev. Ecol. System. 3:1-32.

Estes, R. D. 1972. The role of the vomeronasal organ in mammalian reproduction. Ext. Mammal. 36:315-341.

Fulk, G. W. 1972. The effect of shrews on the space utilization of voles. J. Mammal. 53:461-478.

Gibson, P. S. 1974. Coyotes and related Canis in Arkansas. Coyote Res. News 3:4.

Gorman, M. L. 1976. A mechanism for individual recognition by odour in Herpestes auropunctatus (Carnivora: Viverridae). Anim. Behav. 24:141-145.

Guadagni, D. G. 1968. Requirements for coordination of instrumental and sensory techniques, pp. 36-48, in American Society for Testing and Materials (ed.), Correlation of Subjective-Objective Methods in the Study of Odors and Taste. ASTM STP 440, Philadelphia, Pa.

Hansson, L. 1973. Fatty substances as attractants for Microtus agrestis and other small rodents. OIKOS. 24:417-421.

Hesterman, E. R., and Mykytowycz, R. 1968. Some observations on the intensities of odors of anal gland secretions from the rabbit Oryctolagus cuniculus (L.). CSIRO Wildl. Res. 13:71-81.

Hinde, R. A., and Stevenson-Hinde, J. 1973. Constraints on Learning. Academic, London.

Hood, G. A., Nass, R. D., and Lindsey, G. D. 1970. The rat in Hawaiian sugarcane. Proc. Fourth Vert. Pest. Conf. 4:34-37.

Hornbuckle, P. A., and Beall, T. 1974. Escape reactions to the blood of selected mammals by rats. Behav. Biol. 12:573-576.

Johnston, R. E. 1970. Scent marking, olfactory communication and social behavior in the golden hamster, Mesocricetus auratus. Ph. D. dissertation. The Rockefeller University, New York, N. Y. 145pp.

Johnston, R. E. 1974. Sexual attraction function of golden hamster vaginal secretion. Behav. Biol. 12:111-117.

Johnston, R. E. 1975. Scent marking by male golden hamsters (Mesocricetus auratus). III. Behavior in a seminatural environment. Z. Tierpsychol. 37:213-221.

Jones, R. B., and Nowell, N. W. 1973. Aversive and aggression-promoting properties of urine from dominant and subordinate male mice. Anim. Learn. Behav. 1:207-210.

Kennelly, J. J., Johns, B. E., and Garrison, M. V. 1972. Influence of sterile males on female fecundity of a rat colony. J. Wildl. Manage. 36:161-165.

Keverne, E. G., and Michael, R. P. 1971. Sex-attractant properties of ether extracts of vaginal secretions from rhesus monkeys. J. Endocr. 51:313-322.

Krames, L., Carr, W. J., and Bergman, B. 1969. A pheromone associated with social dominance among male rats. Psychon. Sci. 16: 11-12.

Kverno, N. B. 1964. Forest animal damage research. Proc. Second Vert. Pest. Conf. 2:81-89.

Larue, C. J. 1975. Comparison of the effects of anosmia induced by either peripheral lesion or bulbectomy upon the feeding pattern of the rat. J. Physiol. 70:299-306.

Lee, S. van der, and Boot, L. M. 1956. Spontaneous pseudopregnancy in mice II. Acta Physiol. Pharmacol. Neerl. 5:213-215.

Lehner, P. N., Krumm, R., and Cringan, A. T. 1976. Tests for olfactory repellents for coyotes and dogs. J. Wildl. Manage. 40:145-150.

LeMagnen, J. 1963. Sensorial control in the regulation of food intake. Prob. Actuels Endocr. Nutr. 7:147-171.

Linhart, S. B. 1973. Predator Survey-Western U. S. United States Fish and Wildlife Service. Wildlife Research Center, Denver, Colorado. 54pp.

Lott, D. F., and Hopwood, J. H. 1972. Olfactory pregnancy-block in mice (Mus musculus): an unusual response acquisition paradigm. Anim. Behav. 20:263-267.

Lydell, K. and Doty, R. L. 1972. Male rat odor preferences for female urine as a function of sexual experience, urine age, and urine source. Horm. Behav. 3:205-212.

Mayr, E. 1974. Behavior programs and evolutionary strategies. Amer. Sci. 62:550-659.

Michael, R. D., Bonsall, R. W., and Warner, D. 1974. Human vaginal secretions: Volatile fatty acid content. Science 186: 1217-1219.

Moore, R. E. 1965. Olfactory discrimination as an isolating mechanism between Peromyscus maniculatus and Peromyscus polionatus. Am. Midl. Nat. 73:85-100.

Müller-Schwarze, D. 1971. Pheromones in black-tailed deer (Odocoileus hemiones columbianus). Anim. Behav. 19:141-152.

Müller-Schwarze, D. 1972. Response of young black-tailed deer to predator odors. J. Mammal. 53:393-394.

Müller-Schwarze, D. 1974. Olfactory recognition of species, groups, individuals and physiological states among mammals, pp. 316-326, in M. C. Birch (ed.), Pheromones, North Holland, Amsterdam.

Murphy, M. R., and Schneider, G. E. 1970. Olfactory bulb removal eliminates mating behavior in the male golden hamster. Science 167:302-304.

Murphy, M. R. 1973. Effects of female hamster vaginal discharge on the behavior of male hamsters. Behav. Biol. 9:367-375.

Mykytowycz, R. 1970. The role of the skin glands in mammalian communication, pp. 327-360, in J. W. Johnston, D. G. Moulton, and A. Turk (eds.), Communication by Chemical Signals, Vol. I. Appleton-Century-Crofts, New York.

Mykytowycz, R. 1972. The behavioral role of the mammalian skin glands. Naturwissenschaften. 59:133-139.

Parkes, A. S., and Bruce, H. M. 1961. Olfactory stimuli in mammalian reproduction. Science 134:1049-1054.

Peters, R. P., and Mech, L. D. 1975. Scent-marking in wolves. Am. Sci. 63:628-637.

Preti, G., Muetterties, E. L., Furman, J. M., Kennelly, J. J., and Johns, B. E. 1976. Volatile constituents of dog (Canis familiaris) and coyote (Canis latrans) anal sacs. J. Chem. Ecol. 2:177-186.

Price, E. O. 1975. Hormonal control of urine-marking in wild and domestic Norway rats. Horm. Behav. 6:393-397.

Quay, W. B., and Tomich, P. Q. 1963. A specialized midventral sebaceous glandular area in Rattus exulans. J. Mammal. 44: 537-542.

Ralls, K. 1971. Mammalian scent marking. Science 171:443-449.

Rice, P. R., and Church, D. C. 1974. Taste responses of deer to browse extracts, organic acids, and odors. J. Wildl. Manage. 38:830-836.

Riley, G. A., and McBride, R. T. 1975. A survey of the red wolf (Canis rufus), pp. 263-277, in M. W. Fox (ed.), The Wild Canids, Van Norstrand Reinhold, New York.

Rochelle, J. A., Gaudity, I., Oita, K., and Oh, J. 1974. New developments in big game repellents, pp. 103-112, in Proc. Symp. on Wildlife and Forest Management in the Pacific Northwest, Oregon State Univ., Corvallis.

Shorey, H. H. 1974. Environmental and physiological control of sex pheromone behavior, pp. 62-95, in M. C. Birch (ed.), Pheromones, North Holland, Amsterdam.

Shumake, S. A., Thompson, R. D., and Caudill, C. J. 1971. Taste preference behavior of laboratory versus wild Norway rats. J. Comp. Physiol. Psychol. 77:489-494.

Sperry, C. C. 1941. Food habits of the coyote. U.S. Fish and Wildlife Service Research Bulletin, 4, 70pp.

Stern, J. J. 1969. Copulatory experience and sex odor preferences of male rats. Proc. 77th Annu. Convent., Amer. Psychol. Assn., Washington, D. C. pp. 229-230.

Stern, J. J. 1970. Responses of male rats to sex odors. Physiol. Behav. 5:519-524.

Stevens, D. A., and Saplikowski, N. 1973. Rats' reaction to conspecific muscle and blood: evidence for an alarm substance. Behav. Biol. 8:83-92.

Taylor, K. D., Hammond, L. E., and Quy, R. J. 1974. The response of captive wild rats (Rattus norvegicus) to human odour and to the odour of other rats. Ext. Mammal. 38:581-590.

Tette, J. P. 1974. Pheromones in insect population management, pp. 399-410, in M. C. Birch (ed.), Pheromones, North Holland, Amsterdam.

Thiessen, D. D., Owens, K., and Lindzey, G. 1971. Mechanism of territorial marking in the male and female Mongolian gerbil (Meriones unguiculatus). J. Comp. Physiol. Psychol. 77:38-47.

Thiessen, D. D., and Dawber, M. 1962. Territorial exclusion and reproductive isolation. Psychon. Sci. 28:159-160.

Thiessen, D. D., Regnier, F. E., Rice, M., Goodwin, M., Isaaks, N., and Lawson, N. 1974. Identification of a ventral scent marking pheromone in the male Mongolian gerbil (Meriones unguiculatus). Science 184:83-85.

Thompson, R. D., and Grant, C. V. 1971. Automated preference testing apparatus for rating palatability of food. J. Exp. Anal. Behav. 15:215-220.

Thompson, R. D., Shumake, S. A., and Bullard, R. W. 1972. Methodology for measuring taste and odor preference of rodents. Proc. Fifth Vert. Pest. Conf. 5:36-42.

Tigner, J. R. 1972. Seasonal food habits of Rattus rattus mindanensis in Central Luzon. Ph. D. dissertation. University of Colorado, Boulder, Colorado. 66pp.

Whitten, W. K. 1959. Occurrence of anoestrus in mice caged in groups. J. Endocrin. 18:102-107.

Wittes, J., and Turk, A. 1968. The selection of judges for odor discrimination panels, pp. 49-70, in American Society for Testing and Materials (ed.), Correlation of Subjective-Objective Methods in the Study of Odors and Taste. ASTM STP 440, Philadelphia, Pa.

Wirtz, W. O. 1973. Growth and development of Rattus exulans. J. Mammal. 54:189-202.

Zahorik, D. M., and Johnston, R. E. 1976. Taste aversion to food flavors and vaginal secretion in golden hamsters. J. Comp. Physiol. Psychol. 90:57-66.