

ANAL SAC SECRETION OF THE RED FOX, *Vulpes vulpes*; VOLATILE FATTY ACIDS AND DIAMINES: IMPLICATIONS FOR A FERMENTATION HYPOTHESIS OF CHEMICAL RECOGNITION

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Abstract—Putrescine (1,4-diaminobutane) and cadaverine (1,5-diaminopentane) were identified in the anal sac secretions of the red fox, *Vulpes vulpes*, and of the lion, *Panthera leo*. Anal sac secretion samples obtained over a period of 10 weeks by sampling from within each sac of each of 6 captive foxes were analyzed and putrescine, cadaverine, and volatile fatty acid compositions and secretion pH values recorded. A significant ($P < 0.001$) negative correlation of pH (range 6.5–9.4) with total volatile fatty acid concentration was observed. Secretion compositions are discussed in the context of a fermentation hypothesis of chemical recognition. Secretion samples could not be unambiguously assigned to particular foxes on the basis of simple comparisons of volatile fatty acid profiles alone. Composition differences were noted between secretions obtained at a given time from corresponding right and left sacs.

Key Words—anal sac, volatile fatty acid, putrescine, cadaverine, profile, fermentation, recognition, *Vulpes vulpes*, *Panthera leo*.

INTRODUCTION

Saturated carboxylic acids (C_2 to C_5/C_6) occur together as major volatile constituents of red fox (*Vulpes vulpes*) and lion (*Panthera leo*) anal sac secretions (Albone and Fox, 1971; Albone et al., 1974), Indian mongoose

(*Herpestes auro punctatus*) anal pocket secretion (Gorman et al., 1974), guinea pig (*Cavia porcellus*) perineal gland secretion (Berüter et al., 1974), Rhesus monkey (*Macaca mulatta*) vaginal secretion (Michael et al., 1972), and in the vaginal secretions of other primates, including man (Michael et al., 1974). Microbiological studies have demonstrated the microbial origin of these acids in the red fox, lion, Indian mongoose, and Rhesus monkey secretions mentioned. Only in the case of the Rhesus monkey vaginal secretion has their behavioral significance been investigated in detail, although Gorman (1976) has suggested that the Indian mongoose recognizes conspecifics as individuals on the basis of odor differences between individually characteristic volatile fatty acid profiles of anal pocket secretions.

In this paper we report results concerning variations in red fox anal sac secretion volatile fatty acid and diamine composition, and we discuss the implications of these findings for fermentation hypotheses of chemical recognition.

METHODS AND MATERIALS

Secretion samples were obtained from 6 untamed red fox (Table 1) housed since August, 1973, in two adjoining pens, A and B (each having concreted outside run, 35 m²; covered area, 7.5 m²; height, 2 m), separated by a brick wall completely preventing physical and visual contact between the two pens. Samples, commonly in the range of 25–500 µl, were taken from within each sac via an irrigating cannula (Arnold's Veterinary Products Ltd., 0.762 mm OD; 0.254 mm ID), transferring the sample to a glass vial (chromic acid cleaned) using a disposable syringe. The animals were physically re-

TABLE 1. RED FOX SAMPLED

Fox code	Sex	Pen	Born (spring)
2 ^a	F	A	1973
3 ^b	M	B	1973
4	M	A	1972
5	M	B	1973
6 ^a	F	B	1973
7 ^{a, b}	F	B	1973

^a Foxes 2, 6, 7 were litter-mates. Other foxes are unrelated.

^b Fox 3 was castrated and fox 7 ovariectomized, October 24, 1973.

strained and unseated during sampling. Samples were stored at -20°C prior to analysis. Sampling dates were: 23 Dec. 1974 (code W), 8 Jan. 1975 (code X), 23 Jan. 1975 (code Y), 6 Feb. 1975 (code Z), 20 Feb. 1975 (code A), 5 Mar. 1975 (code B). Secretion samples are coded with a number identifying the fox (Table 1), a letter identifying the sampling date and R (or L) indicating right (or left) sac.

Volatile fatty acids were analyzed using a Pye-Unicam 104 gas chromatograph (FID) with a 2.3-m \times 4-mm (ID) silanized glass column of 3.5% w/w Pegosperse S-9 (Glyco Chemicals Inc.) and 0.35% w/w orthophosphoric acid on Chromosorb W-AW, 60/80 mesh (nitrogen carrier, 30 ml/min; column temperature 110° , isothermal; injector temperature 230°) by on-column injection of untreated aqueous secretion, or of secretion diluted 1:1, v/v, with aqueous *n*-hexanoic acid (0.018 M) as internal standard. Peak areas were estimated by cutting and weighing xerox copies of chromatograms. Gas chromatography of untreated secretion was preferred to that of the diethyl ether extract of acidified secretion, particularly where very small samples were available. A standard mixture of volatile fatty acids adjusted to various pH values up to 9.8 with ammonia yielded identical volatile fatty acid chromatograms. Gas chromatograms of diethyl ether extracts of selected acidified secretions were closely comparable with those obtained from untreated secretion in regard to the volatile fatty acid peaks, save that the more water-soluble acids (particularly acetic acid) were underestimated because of incomplete extraction.

Amines were detected and identified following derivatization with 1-dimethylaminonaphthalene-5-sulphonyl (dansyl) chloride (BDH Chemicals Ltd.). Authentic putrescine and cadaverine were purchased from Koch-Light Laboratories Ltd. and Ralph Emanuel Ltd., respectively. For analytical purposes, anal sac secretion (10 μl) was added to dansyl chloride (100 μl , 30 mg/ml acetone solution) followed by distilled water (30 μl) and sodium bicarbonate (50 mg). After standing (16 hr), proline (15 mg) was added and the sample left a further 2 hr. Distilled water (1 ml) was added and the sample extracted by agitation with ethyl acetate (2 ml) followed by centrifugation. The ethyl acetate extract was concentrated to 250 μl under nitrogen and examined (5 μl) by thin-layer chromatography (TLC).

TLC was performed with chloroform-triethylamine, 5:1, v/v, and with cyclohexane-diethyl ether, 1:9, v/v, on Merck silica gel 60 (0.25 mm) pre-coated plates for analytical purposes and on acetone preeluted Kieselgel G (0.5 mm) plates preparatively. Dansyl chloride derivatization of a standard mixture of all common amino acids revealed no artifacts moving in the region of putrescine and cadaverine didansyl derivatives. Analytical plates were sprayed with isopropanol-triethanolamine, 4:1, v/v, immediately after chromatography, dried over silica gel under vacuum at room temperature

for 16 hr and fluorescence assayed by scanning with a Vitatron densitometer, Model TLD 100 (507 nm filter, 0.25 mm diaphragm, scan speed 1 cm/min).

Mass spectrometry was performed using an AEI MS 902 mass spectrometer (direct insertion probe), source temperature 260–280°.

pH measurements were conducted, where sufficient sample was available, using a microelectrode (Activion Glass Ltd., Model 003-11-306) with an Electronic Instruments Ltd pH meter (Model 38B).

RESULTS

Components corresponding in TLC mobility to authentic *N,N'*-didansylputrescine and to *N,N'*-didansylcadaverine, obtained by subjecting dansylated fox anal sac secretion (2WL, 160 μ l) to preparative TLC consecutively with chloroform–triethylamine, 5:1, and with cyclohexane–diethyl ether, 1:9, yielded the following mass spectral data ($m/e \geq 150$):

Component 1: R_f (CHCl₃/Et₃N, 5:1) 0.42; (C₆H₁₂/Et₂O, 1:9) 0.24, m/e ; 555 (12.3), 554 (M⁺, 40.0), 172 (13.9), 171 (100), 170 (82.2), 169 (45.7), 168 (45.7), 167 (8.7), 155 (17.5), 154 (21.0).

Component 2: R_f (CHCl₃/Et₃N, 5:1) 0.54; (C₆H₁₂/Et₂O, 1:9) 0.28, mass spectrum, very weak, with molecular ion, m/e 568 and intense m/e 170, 171.

These spectra indicate *N,N'*-didansylputrescine and *N,N'*-didansylcadaverine, respectively (Seiler et al., 1970; Creveling et al., 1968). Components of identical TLC properties were also observed in dansylated lion (*Panthera leo*) anal sac secretion (4-year-old male, sampled August, 1974). In this case, mass spectrometry yielded a strong *N,N'*-didansylcadaverine spectrum, m/e ; 569 (9.7), 568 (M⁺, 25.7), 250 (8.6), 172 (14.5), 171 (100), 170 (59.7), 169 (51.4), 168 (29.8), 155 (10.4), 154 (13.2), although insufficient component corresponding to the *N,N'*-didansylputrescine TLC zone was available to yield a satisfactory mass spectrum.

Two-dimensional TLC using the above solvent systems with selected dansylated fox and lion anal sac secretion samples confirmed that the fluorescent spots running with *N,N'*-didansylputrescine and *N,N'*-didansylcadaverine in chloroform–triethylamine each yielded predominantly one spot in the second dimension and that these corresponded with the same authentic compounds.

Anal sac secretion volatile fatty acid profiles are depicted in Figure 1, and total volatile fatty acid, putrescine, and cadaverine concentrations together with secretion pH values are given in Table 2. Blank entries indicate that insufficient secretion was obtained. In some cases, the secretion was seen

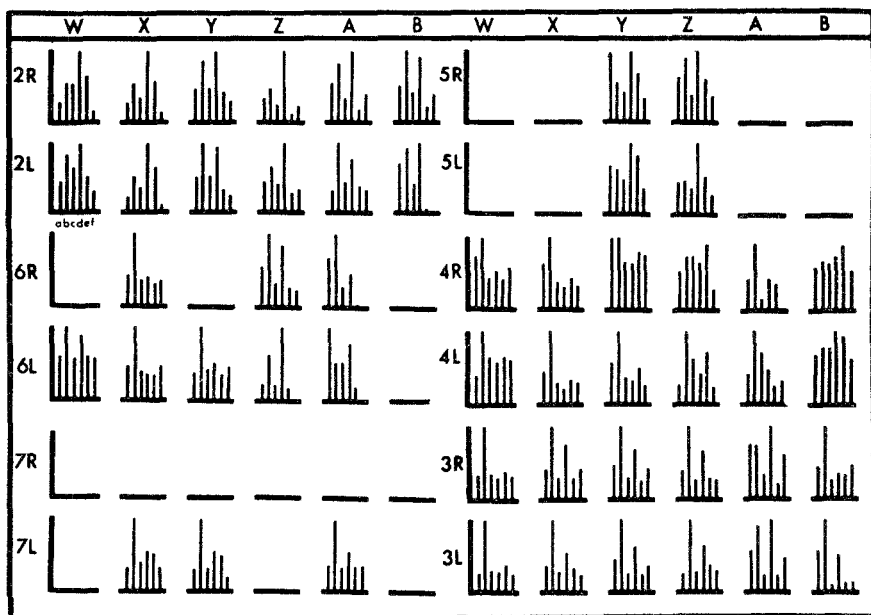


FIG. 1. Red fox anal sac secretion volatile fatty acid profiles. Each sample is coded with a number identifying the fox (Table 1), a letter indicating the sampling date, and R or L indicating right or left sac. Each profile records in sequence the relative molar concentrations of (a) acetic acid (concentration $\times 0.1$), (b) propionic acid, (c) isobutyric acid, (d) *n*-butyric acid, (e) isovaleric acid, (f) isocaproic acid. Blank entries indicate insufficient sample was obtained.

to be voided by the animal before sampling began. The volatile fatty acid profiles were calculated on the basis of the following identifications (in order): acetic, propionic, isobutyric, *n*-butyric, isovaleric, and isocaproic acids. The isovaleric acid peak may contain unresolved 2-methylbutyric acid (Albone and Fox, 1971). The *n*-butyric acid peak sometimes overlapped a poorly resolved unidentified component, and in such cases the two components were quantified together as *n*-butyric acid for purposes of profile comparison as it was not possible to estimate accurately the contribution of each component to the composite peak. When a composite peak was observed, its form was usually closely similar for corresponding right and left sac secretions.

n-Valeric acid was present in a number of samples, but always as a minor component and was not tabulated in the profiles.

DISCUSSION

In spite of the limited number of samples examined, a visual inspection

TABLE 2. RED FOX ANAL SAC SECRETION COMPOSITIONS: pH VALUES AND TOTAL VOLATILE FATTY ACID (VFA), PUTRESCINE [Put], AND CADAVERINE [Cad] CONCENTRATIONS

Sample ^a	pH	[VFA] ^b (mM)	[Put] (mM)	[Cad]/[Put]	Sample ^a	pH	[VFA] ^b (mM)	[Put] (mM)	[Cad]/[Put]	Sample ^a	pH	[VFA] ^b (mM)	[Put] (mM)	[Cad]/[Put]
2RW	8.5	—	—	—	2LW	7.6	92	19	0.36	6RW	8.5	14	4	0.75
2RX	8.1	44	9	0.31	2LX	8.7	39	6	0.21	6RX	8.5	14	4	0.75
2RY	6.6	132	29	0.08	2LY	7.4	137	30	0.25	6RY	—	—	—	—
2RZ	6.6	102	18	0.34	2LZ	—	51	13	0.19	6RZ	—	—	—	—
2RA	6.5	146	7	0.01	2LA	8.2	30	4	0.00	6RA	7.1	31	8	1.7
2RB	—	106	10	0.21	2LB	—	49	9	0.53	6RB	—	—	—	—
3RW	8.3	72	10	0.15	3LW	8.7	25	4	0.33	6LW	8.7	9	3	0.20
3RX	8.2	60	13	0.26	3LX	7.3	114	25	0.05	6LX	9.0	19	2	1.4
3RY	8.1	60	8	0.25	3LY	8.3	—	8	0.32	6LY	—	—	—	—
3RZ	7.0	126	26	0.03	3LZ	8.1	45	8	0.09	6LZ	—	—	—	—
3RA	7.4	35	8	0.85	3LA	—	34	8	0.04	6LA	—	32	7	0.27
3RB	—	17	—	—	3LB	—	39	5	0.26	6LB	—	—	—	—
4RW	8.4	25	2	2.7	4LW	8.4	21	2	3.3	7LW	—	—	—	—
4RX	8.8	13	0.8	2.3	4LX	8.6	15	2	2.8	7LX	8.9	26	2	<0.1
4RY	9.4	6	0.5	3.2	4LY	8.6	7	0.6	3.9	7LY	9.0	34	—	—
4RZ	—	7	0.9	3.5	4LZ	—	12	1	2.9	7LZ	—	—	—	—
4RA	8.7	8	0.6	0.74	4LA	8.6	17	4	3.2	7LA	—	20	2	0.20
4RB	—	14	1.5	2.3	4LB	—	29	3	2.9	7LB	—	—	—	—

^a Samples are coded with a number identifying the fox (Table 1), a letter indicating sampling date, and R or L indicating right or left sac.

^b Calculated from gas chromatography profile data.

of the volatile fatty acid profiles (patterns of abundance), Figure 1, reveals the following features of importance.

1. The profiles of secretions obtained from the two sacs of a given fox at a given time were usually similar (e.g., 2XR/2XL, 3ZR/3ZL, 4XR/4XL), but not invariably so (e.g., 2BR/2BL, 3BR/3BL, 4AR/4AL). Odor differences between the secretions of the two sacs of a given animal at a given time have not previously been considered.

2. The profiles of secretions taken from a particular sac of a particular animal may remain relatively unchanged on consecutive sampling dates (e.g., 3XR/3YR/3ZR, 7XL/7YL), or they may change between sampling dates (e.g., 3ZR/3AR/3BR).

3. The short-term variability in the profile of a given animal may be greater than the profile difference between animals (e.g., 3ZR/6ZR), so that *it is not possible to assign unambiguously a particular sample to a particular fox on the basis of a simple visual profile comparison*. An exploratory computer analysis using a multivariate profile of the six peaks has revealed some evidence of a degree of clustering within the samples of some foxes (fox codes 2, 5, 7), whereas the others appeared to be randomly scattered. These studies are continuing.

4. No obvious features distinguish the profiles of the foxes from pen A from those from pen B (Table 1), nor the intact from the castrated and ovariectomized animals, even though sampling was conducted during the breeding season [January, early February (Burrows, 1968; Creed, 1972)]. We observed no evidence of pregnancy in the study foxes, however. Although the possible existence of such fox anal sac secretion distinguishing features is the subject of continuing study, the recent finding by Doty and Dunbar (1974) that, for the beagle, anal sac secretions of estrous bitches were no more attractive to males than those of diestrous bitches, renders it less likely that sexually related effects will be found.

Throughout, the major amine component of anal sac secretion was ammonia, present in greater, and frequently in considerably greater, concentrations than those of the volatile fatty acids. Smaller concentrations of putrescine and cadaverine were also present and the relative proportions of these diamines also exhibited considerable variation, including right sac/left sac variation, e.g., 3AR/3AL (Table 2). Interestingly, all fox 4 samples (R and L) examined, except 4AR (ratio 0.74) exhibited a molar ratio of cadaverine to putrescine in the range 2.3–3.9, mean 3.0, $n = 11$, and were thus distinguished from all fox 2 (R and L) samples, range 0–0.55, mean 0.23, $n = 11$, and all fox 3 (R and L) samples, range 0.03–0.84, mean 0.24, $n = 11$.

When pH values and total volatile fatty acid concentrations of different secretions (Table 2) were compared, further differences were revealed between

certain secretions even of closely similar volatile fatty acid profile (e.g., 3ZR/3ZL).

The pH range of fox anal sac secretion extended from 6.5 to 9.4 and the total volatile fatty acid concentration from 6 mM to 146 mM. A linear regression of pH on total volatile fatty acid concentration was obtained, slope -0.015 pH unit/mM/liter and intercept (0 mM) 8.9 pH units (correlation coefficient -0.835 , $n = 30$, $P < 0.001$). The secretion pH values, being intermediate between the pK_a values of the volatile fatty acids (pK_a , 25°, acetic, propionic *n*-butyric isobutyric, isovaleric, and isocaproic acids being 4.76, 4.87, 4.82, 4.86, 4.78, and 4.85, respectively) and those of the amines [pK_a , 25°, ammonia, putrescine, and cadaverine being 9.25, 10.81 (pK_2 9.63), 10.93 (pK_2 10.05) respectively] indicated that the secretion acids and amines were present in solution predominantly in their odorless ionic forms. The free (un-ionized) acids and amines contribute to the odor of the secretion and, for a given acid/amine mixture, for every pH unit increase an approximately 10-fold increase in free amine and an approximately 10-fold decrease in free acid concentration results. The concentrations of any volatile nondissociable species (not investigated here) are pH independent. In this way the pH controls the odor of a given mixture by exerting differential effects on the partial vapor pressures of odorous acids, amines and nondissociable species.

The volatile fatty acids present in red fox anal sac secretion are the products of the resident microflora (Gosden et al., 1975; Albone et al., 1974) and it is most likely that the diamines present are, at least in part, similarly formed particularly by the sac *Clostridia* (Brooks and Moore, 1969; Hyatt and Hayes, 1975), although this has yet to be confirmed.

No evidence suggests that the two anal sacs of the fox are emptied to the same extent when secretion is expelled. Indeed, secretion volume differences were frequently noted between corresponding sacs so that, e.g., fox 7 never yielded sufficient secretion for analysis from its right sac, while the left sac yielded satisfactory samples on three out of six occasions. We therefore suggest that differences in secretion pH, including the substantial left sac/right sac differences frequently observed (Table 2), may reflect differences in secretion incubation (residence) time in the sac. This cannot be proved until techniques are available to follow the time dependence of sac processes without incurring the disturbance caused to the sac microenvironment by the sampling method presently employed. However it is commonly observed that incubations of proteinaceous substrate lead to increased pH with time whereas pH decreases are noted in carbohydrate fermentations.

Gorman (1976) has advanced a fermentation hypothesis for chemical recognition for the Indian mongoose by suggesting that this animal recognizes conspecifics as individuals on the basis of odor differences between individually characteristic profiles of microbiologically produced volatile fatty acids present in their anal pocket secretions.

As with the Indian mongoose, these same volatile fatty acids are also produced by fermentation in the anal sac secretions of the red fox and the lion and are present in the anal sac secretions of the bush dog, *Speothos venaticus*, of the tiger, *Panthera tigris*, of the maned wolf, *Chrysocyon brachyurus*, and of the domestic dog, *Canis familiaris* (Albone, unpublished observations) as well as of the domestic cat, *Felis catus* (Michael et al., 1972), although in these cases a microbial origin has yet to be investigated. Further emphasis of cross species similarities between such analogous fermenting systems is provided by the finding that the anal sac secretions of two such diverse carnivores as the red fox and the lion not only contain the same volatile fatty acids and the same diamines as major odorous constituents but also support closely similar microflora (Gosden et al., 1975).

Although the sensitivity of mammals to the odors of these diamines has yet to be studied, it is known that the domestic dog is sensitive to the volatile fatty acids (Moulton et al., 1960) and that the Indian mongoose can distinguish between different mixtures of these acids by olfaction (Gorman, 1976). Questions arise concerning the ways in which such odorous substances, the microbial formation of which appears to depend little on sex, sexual status or even, within limits, on species,¹ might acquire ecochemical significance.

A fermentation hypothesis of chemical recognition offers one possibility. By processes of cross-infection, a group of animals living together would be expected to come to share a common microflora characterizing that group. Even when the species of microorganisms are narrowly defined, the possibility of many biochemical strains provides sufficient group-distinguishing potential. The hypothesis argues that if these microorganisms produce substances detectable by the mammal in question, the odors of individuals from a particular group would possess certain recognizable common features characteristic of that group and its shared microflora (Albone et al., 1974). It is known that characteristically different volatile metabolite profiles are produced by different strains of microorganism incubated under standard conditions (Lewis et al., 1967) but the situation is complicated by observations that incubation (residence) time can affect profile (Moore et al., 1966), as can substrate (primary secretion) composition variations. Gorman (1976) has advanced a particular example of this fermentation hypothesis in relation to individual chemical recognition in the solitary Indian mongoose.

Results presented in this paper give an indication of the variability of odor profile to be expected in fermenting systems analogous to the red fox anal sac and point to the importance of such factors as pH variation and right sac/left sac differences which have not previously been considered. These observations make it more difficult to believe that odor profiles of fermenting

¹ Gross differences in anal sac secretion volatile composition with species do occur, e.g., the dominance of C₄ and C₅ thiols in striped skunk (*Mephitis mephitis*) anal sac secretion (Andersen and Bernstein, 1974; Bernstein, 1974).

systems possess sufficient stability to form a basis for chemical recognition, although the proof must await further bacteriological, behavioral, and chemical studies, and they raise doubts which merit further examination in relation to Gorman's Indian mongoose studies.

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