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Chemocommunication among Domestic Cats, Mediated by the Olfactory and Vomeronasal Senses

I. Chemocommunication

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With 9 figures

Received: 5 January 1976

Accepted: 29 April 1976

Abstract

Chemocommunication functions are known in many social mammals, such as gerbils, hamsters, and deer. But also mammals known as at least partly solitary do communicate by chemical signals. The existence and use of pheromones in domestic cats was the subject of this study. It turned out that male and female cats spent much time in exploring their own and foreigners' urine and skin gland secretion rubbed off on several objects. Male receivers performed sniffing and flehmen more frequently than ♀♀ on the same urine, whereas female cats paid more attention to skin gland secretion. Both urine and cheek gland secretion of the female donor appeared to contain pheromones which inform the tomcat about her hormonal phase.

Introduction

The purpose of this study is to establish the existence of pheromones and their use in social or sexual context by domestic cats. Therefore the explorative behaviour in general has been observed and recorded in a semi open-field situation, especially where marking behaviour, such as urine spraying and rubbing was displayed.

Urine spraying is a well-known and often daily recurring habit in felids, and many domestic tomcats form no exception to this rule. Surveys about this matter have been published by EWER (1968), LEYHAUSEN (1973 a) and VERBERNE and LEYHAUSEN (1976).

The function of urine marking in felids has been studied mainly in a territorial context, where the age of the urine is a significant cue for the individual trespassers (LEYHAUSEN and WOLFF 1959, SCHALLER 1967, EATON 1974 and DE BOER in prep. 1).

Urine is most likely to elicit flehmen behaviour in tomcats after they have sniffed thoroughly. This holds for many feline carnivora (SCHNEIDER 1932, VERBERNE 1970, LEYHAUSEN 1973 a). Since in other mammals (SCHNEIDER 1932, DAGG and TAUB 1970, ESTES 1972, EATON 1974) it has been shown that

*) Supported by a grant from the Foundation for Fundamental Biological Research (BION), subsidized by the Netherlands Organisation for the Advancement of Pure Research (ZWO).

♂♂ display flehmen more frequently than ♀♀, we will compare occurrence and frequency of sniffing and flehmen in male and female domestic cats. This is the more important as sexual differences in the conditions under which both producing and exploring urine in ♂♂ and ♀♀ will inform us better about the rules of chemocommunication among cats. Whether rubbing cheek, chin or other parts of the head, mostly considered as a marking act, really leaves a scent, or better: a chemical signal, has until now been an unanswered question. Therefore the next part of the study deals with the occurrence of rubbing and also rolling and the subsequent reactions of the next exploring animal on the newly rubbed spot. The following step is to inquire whether the exploring animal, after olfactory exploration of a rubbed spot also answers with rubbing the same object.

The next part is focused on processes comparable with habituation. When an exploring cat, after having sniffed and flehmed a scentsource, returns to the same scent, it will sniff and flehm again, but the frequency of the sniffing and flehmen bouts within a pattern as well as the duration of sniffing declines (VERBERNE 1970, VERBERNE et al. 1974).

The reason to investigate features comparable with habituation again is that habituation forms an intrinsic part of the explorative behaviour (VOSSEN 1966). Another reason is based on the question whether these processes as a result of repeated exploring an olfactory stimulus, pass similarly in ♂♂ or ♀♀.

In the last section of our study we investigated the significance of urine and skin gland secretion as a pheromone carrier providing information to the receiver about the phase of the estrous cycle of the female donor-cat.

Materials and Methods

1. Animals

Our animal stock started in 1969 with several cats given to us. Breeding resulted in a healthy group of ♂♂ and ♀♀, enriched sometimes by new gift animals. Some tomcats had been castrated, others were castrated after one or several years. One ovariectomised ♀ arrived in this condition.

The animals were held in small groups of ♂♂ only, ♀♀ only or of both sexes together. The cages measured $2 \times 2 \times 3$ m, and most of the cats could roam through an even larger outer cage. A total number of 23 cats from 8 months to 4 years old were used during a few years in the experiments in about 1,200 observations.

2. Observations

Three observations were done in the course of 4 years in different observation rooms in sequence, but otherwise the situations were similar: an empty room of at least 20 m³ with a few objects, such as a chair, table or trunk. The observer was sitting in the room, which evoked some social and explorative behaviour, such as calling, rubbing and sniffing the observer. In the last room, occupied since the beginning of 1973, the observer was sitting outside the room, watching the animal through a glass wall. Even then some social behaviour with respect to the observer was evoked. The individual cats were observed consecutively and usually in the same sequence. Observations were usually done once a week; in exceptional cases, in a more frequent schedule, up to three times a week.

3. Scent stimuli

- a. The scent stimuli were produced by the visiting cats, either a spray of urine or cheek gland secretion rubbed on protruding objects. The donor as well as the location and age of the scent were documented carefully.

- b. In the last set of observations we placed two wooden pegs symmetrically in the observation arena. One peg was rubbed by one and the same cat each time by 8 strokes of the cheek against the top of the peg. The other peg was clean or not rubbed during the last four weeks. The place of each peg at the left or the right side of the room was chosen at random. The donor cat (Isodora) was always very likely to rub the peg when the observer entered her cage in the early morning and caressed her. That means that rubbing in this situation had, at least partially, a social significance.

It is not clear whether she would have left behind other secretions in case she had rubbed when motivated only to scent-mark. Unfortunately she rubbed an object only once during exploration of the observation room (30 observations).

- c. In some series of observations an additional stimulus, e.g. urine was placed by the observer beforehand, but usually the experimental set-up was as follows:

Trial 1: The situation described above; duration 15 min. Subsequent to this observation — where an animal explored floor, walls, corners etc. more or less completely — followed:

Trial 2: A separate stimulus was brought into the observation room, such as urine, butyric acid etc. Cotton wool or wooden pegs served as carriers. In many cases the animal approached the scent source and sniffed, followed by other reactions. In case the animal did not approach the scent source the stimulus was presented just in front of the nose. Almost all cats were willing to explore the stimulus.

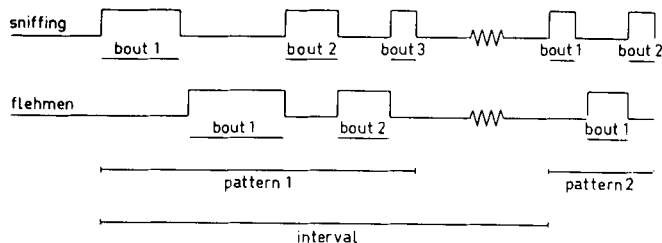
The advantage of the procedure used in trial 2 is, that almost every animal receives the same scent after a period of rest and grooming during the last min of trial 1 (cf. Results below p.94). In this way the stimulus presentation is comparable for all cats. The duration of trial 2 generally did not exceed 5 min and the session was actually terminated when the animal stopped responding to the stimulus and went away.

4. Data collection

The observations of the successive behavioural acts were noted on prepared sheets, later on recorded by means of a 20 point Esterline Angus recorder and since 1973 computerised.

In the two latter cases occurrences, durations, frequencies and transitions of the observed acts were recorded accurately.

Abbreviations: S: Sniffing, F: Flehmen, L: Licking lips and mouth, H: Headshaking, Ru: Rubbing, Ro: Rolling, Li: Licking an object, No.: Number.



length sniffing of pattern 1 = bout 1 + bout 2 + bout 3

length sniffing of pattern 2 = bout 1 + bout 2

length flehmen of pattern 1 = bout 1 + bout 2

length flehmen of pattern 2 = bout 1

Fig. 1: Examples of a Sniffing (S) and Flehmen (F) pattern, represented on two separate lines. The first pattern, consisting of 3 S bouts and 2 F bouts is followed after a certain interval by the next S-F pattern, consisting of 2 S and 1 F bouts

Definitions: We will define here two terms, which will be used frequently in this paper (cf. Fig. 1).

1. a *bout* is a non-interrupted act, e.g. a sniffing or a grooming act;
2. a *pattern* is a non-interrupted series of different acts, which are related to the same stimulus. The most patterns involved in this study are Sniffing-Rubbing and Sniffing-Flehmen-Licking-Headshaking.

Particular experimental techniques as well as details in analysing the behaviour will be described at the appropriate points in the text.

Statistical analysis was always executed with a two-tailed test.

Results

1. Exploratory Behaviour

A cat released in the observation room generally starts with looking around and walking slowly with the nose to the floor. It learns rather quickly where to find the interesting corners with fresh or old urine markings. (One corner was very rarely sprayed and at the same time explored very incidentally by the visitors).

Transmission of the scent by air was sometimes obvious, but only in exceptional cases, and thus seemed part of the reason why they preferred to explore special corners where they sometimes found spots of urine about 7 days old. The visual cue of the yellow spot or the dark blood drop appeared to work; also other dark marks were approached and sniffed attentively. During an observation period of 15 min, the activity of all cats showed the same tendency (Fig. 2): locomotion and visual and olfactory exploration as

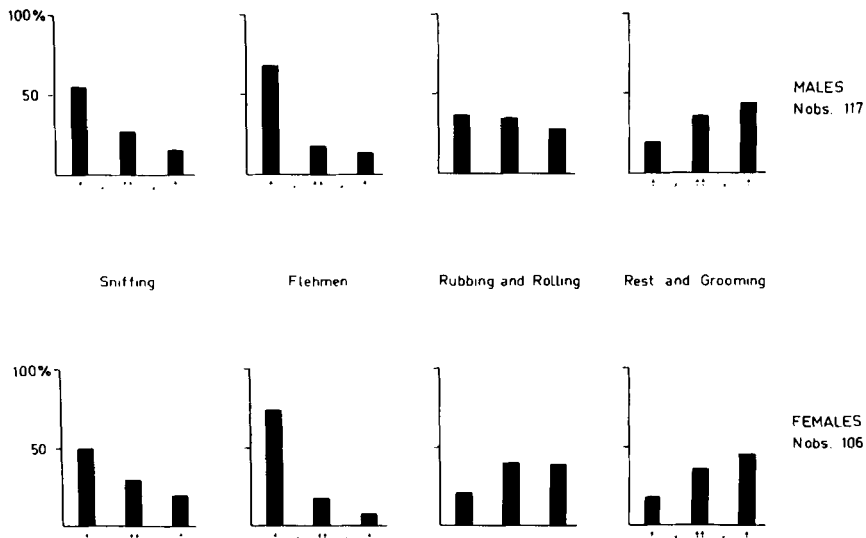


Fig. 2: Performance of olfactory exploration, Flehmen, Rubbing and Rolling, and Rest and Grooming in the course of 15 min during trial 1 by 9 ♂♂ (A) and 8 ♀♀ (B). The duration of the four categories of behaviour are represented for the first, second and third 5 min in %. An * points to a significant increase or decrease of one particular behaviour between the two sequential epochs (sign test $P < .05$). The tendencies of the four categories are also significant in most of the individual animals

well as F decreased gradually and were substituted by rest, play and grooming. Ru and Ro frequencies, however, did not show any trend, neither in ♂♂ nor ♀♀ (Fig. 2). Only some of the animals called, some right from the start and obviously as a result of excitement: during exploration calling waned gradually. Some ♀♀ persisted in calling throughout the observation time, especially those pregnant or those raising their kittens; on the other hand, ♀♀ in heat as

a rule did not call. But calling frequencies of ♀♀ could also be extremely high (> 200 per 15 min) without any obvious reason. Some animals called to the observer at the end of the observations (or when entering the room) and unmistakably showed requests to be freed.

In conclusion, calling under these circumstances does not seem to bear much significant information to the observer about the animal's exploratory behaviour.

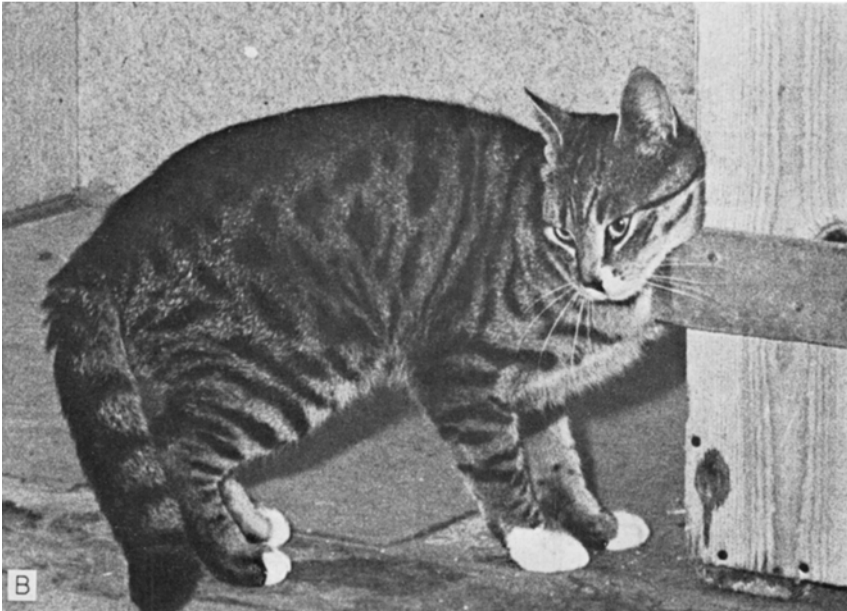
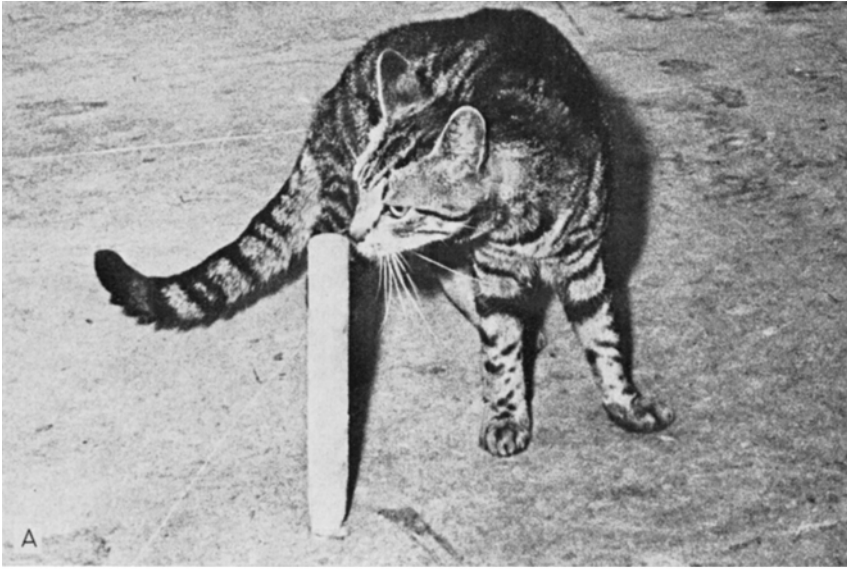


Fig. 3: A cat, exploring a peg (A) and rubbing an object (B)

2. Scentmarking

2.1. *Urine spraying*. — Urine spraying was performed by almost all tomcats during the observation period. Some tomcats sprayed very rarely, others did it almost every time they visited the room. It seemed that urine marking did not release squirting in other tomcats. There were no indications that they tried to cover the markings of the preceding animal with their own urine. (Part of the results were presented at the Intern. Ethological Conference, 1973, and will be described in detail elsewhere. DE BOER in prep. 1).

Some of the tomcats did not squirt, but produced small amounts of urine followed by more or less serious attempts to bury it. ♀♀ sprayed very rarely and were also able to produce small amounts of urine which was followed by scraping movements.

2.2. *Rubbing*. — Ru was performed by a number of cats — male and female — in the semi open-field situation (Fig. 3), but the individual frequencies differed remarkably. Cats rub in different ways.

- a) Ru the point of the nose very carefully on a protruding tip.
- b) Cheekru is usually performed along a line from the corner of the mouth to the ear. From that position they return to the starting position, the corner of the mouth. During intensive Ru the mouth is sometimes open and the upper teeth are unsheathed.
- c) The rim of the wooden trunk in the observation room often released a Ru of the upper side of the head. The cats start in standing position on four paws and rub their heads while raising their hindfeet.
- d) Another way of Ru is performing strokes from the chin to the throat especially on a low lying object.
- e) When walking along a rim a cat can rub its side against it; this is often followed by Ru the tail along the object. Ru the upper side of the tail is sometimes displayed when they have the opportunity to walk under a horizontal object, e. g. a chair.

2.3. *Rolling*. — Ro from the right to the left side in lying position is sometimes displayed and usually accompanied by L and H.

Breast and inner side of the forepaws are preferentially licked during Ro. Also H is involved in Ro activities.

Transitions from Ru to Ro may happen in a stage of high intensity. ♂♂ and ♀♀ perform Ru and Ro in the same way; neither did they show any systematic difference in frequencies throughout the numerous observation periods. Some ♂♂ rolled infrequently, others performed it regularly and frequently. The three ♀♀ (out of the group of 8) who performed it most frequently showed a clustering of Ro throughout an epoch of 4—6 weeks. Ru and Ro, as a reaction to scents will be described in Ch. 3.

2.4. *Other marking acts*. — We observed a few times that two of our tomcats pressed from standing position some clear transparent viscous droplets on the wall, apparently coming from glands under the tail. The secretion had a very strong "tomcat" smell. We did not have the opportunity to observe from which gland the secretion was produced, but it is unlikely that it came from the bilateral circumanal glands, as this secretion is not transparent but yellow-brown coloured and has a different smell.

3. Reactions to marked spots

We will now present the reactions on: 1) urine, sprayed or put down in small quantities by the male visitors; 2) pegs rubbed by one and the same

female cat; 3) objects rubbed by one or more animals, irrespective of their sex. The "receivers" were ♂♂ and ♀♀. We did not differentiate between ♀♀ in either pregnant, lactating, non lactating or estrous phase as we found no indications for significant differences in responses during these periods (Mann Whitney U-test).

3.1. Reactions to urine. — In by far most of the cases urine released F after careful S; the cats flehmed readily on fresh and one week old spots but rarely (though still) on older scents.

It can be stated in general that the intensity of F (given in frequency) decreased in parallel with the age of the scent (DE BOER in prep. 1). F on own urine was observed frequently, but seldom directly after having produced it, be it by squirting or from squatting position. The animals usually went off without turning and S or, if they turned and inspected their urine, they made more or less serious attempts to bury it.

A few animals responded after S with Ru and Ro (see also 4. Conflicting reactions).

In order to examine sexual differences in responding as regards S and F we have to analyse the complex F pattern. The most complete sequence of acts

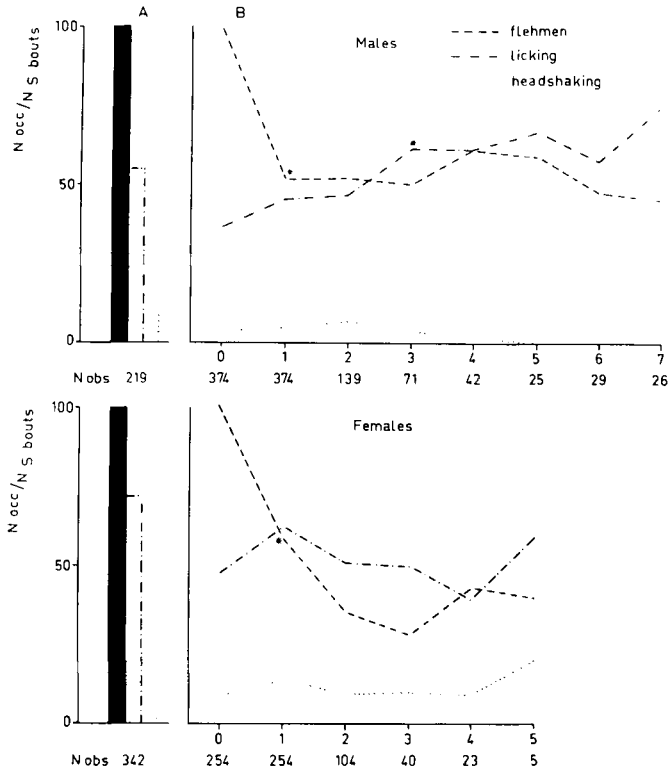


Fig. 4: Data from single and repetitive Sniffing (S), Flehmen (F), Licking (L) and Headshaking (H) patterns for 12 ♂♂ and 11 ♀♀. Abscissa: order number of S repetitions in one pattern; N obs.: Number of observations. Ordinate: N occurrences divided by N of S per order number. A: N of single S-F patterns showing occurrences of each of the four component behaviours S-F-L-H. B: N of repeated S-bouts in one pattern, not interrupted by behaviours other than F, L and H, on the same scent. The repetition numbers of S are represented in the N obs. on the abscissa. If less than 20 observations were made, the observations of the next order number were added. An * points to a significant ($P < .05$) decrease or increase of the frequency in the repetition proper as compared with the zero order number (sign test)

will be described here. An exploring cat cursorily sniffs a scent source, e. g. a freshly squirted urine mark. In this case the ears are directed forwards. The first exploration is either followed by a walk-away and a further exploration of the environment, or by a second stage of S. This S is characterised by a long intensive S (Dur up to 24 s), the point of the nose contacts the scent, ears are turned backwards, eyelids sometimes narrowed. Movements of the tongue are sometimes visible. The tongue is moved rhythmically along the roof of the mouth, seldom up to the point of the nose. S and sucking noises can be heard in some cases. When the scent source had dried up one can see that during this type of S the spot is moistened with the tip of the nose. After all these preparations the animal raises its head, opens the mouth — the upper and/or lower canine teeth are sometimes visible — and keeps this posture several seconds (1—16 s). This posture is followed either by again S and a next repetition of F, or by licking (L) movements along nose, lips and corners of the mouth and by (more rarely) head-shaking (H). In other situations the cats walk away and devote their interest to other things. The patterns S, F, L and H are represented in Fig. 4 in the same way as has been done earlier for some felids (VERBERNE 1970). Single F patterns (A) in connection with L and H are given separately to those where the first F bout is immediately followed by a second S on the same scent source (B).

The patterns given in Fig. 4 are results of 11 ♀♀ and 12 ♂♂. For each of the individual animals the same structure of the patterns can be found.

The occurrence of H is so low that one could wonder whether it is really an intrinsic part of the S-F pattern, or simply a coincidence. Moreover, the occurrence in the total observations is much higher and apparently caused by other factors. Therefore we measured the interval between F_1 and H and the same H with the next one — F_2 — under the condition that F_2 is not part of the same pattern as F_1 and that H occurs only once between the two S-F patterns.

We took at random a sample of 50 observations from 5 ♂♂ and 9 ♀♀. The mean interval between F_1 and H is 55 s, whereas that between H and F_2 is 154 s. The sign test applied to the paired intervals gave a P value $< .005$. The following conclusions can be drawn (Fig. 4): 1) The No. of single F patterns in ♂♂ is smaller than that of the repetitions. For the ♀♀ we found the reverse. The sexual difference appeared to be significant (χ^2 test $P < .001$). 2) In single F patterns F is more frequently followed by L and H than the first F bout of a repetition series in both series. 3) During the course of the repetitive S bouts in one pattern the frequency of F declined, whereas that of L and H increases. After a number of repetitions the frequency of F with respect to that of S is restored somewhat, whereas L decreases again. We found the moment of recovery different according to the individual animal; as a consequence the picture shows a fluctuating line, as all data are presented together. No systematic differences between the two sexes could be noticed in this respect. 4) The No. H occurs less frequently than L, both in single and repetitive patterns. This holds for both sexes. 5) The duration of F during the repetition rates in one pattern and during the course of the observations are not different as was reported earlier (VERBERNE 1970, VERBERNE et al. 1974). The frequency of F in one pattern thus seems to serve as a parameter of the intensity of the reaction in both ♂♂ and ♀♀.

These data confirm those of 1970 perfectly, as far as the ♂♂ are concerned.

We will discuss the functional significance of the separate acts in this pattern in a second stage (part II).

A separate experiment was then undertaken to analyse the *sexual differences* in the frequency of displaying F as was given under 1. We compared two groups of animals in two different observation rooms; the test situation in each set, however, was strictly comparable for all animals involved. We did not present urine of ♀♀ in estrous in this experiment, to avoid the influence of a possible differing interest in the scents depending on the sex of the donor, resp. receiver.

Table 1: Sexual differences in Flehmen (F). From left to right: the animal and its sex; No. obs: the number of observations; No. occ F: the No. obs where F had been displayed; No. F/No. occ F: the ratio No. F bouts to the No. occ F; No. sc s: the No. scent sources which released F; No. rep F bouts: the No. repetitive F bouts in one pattern; No. returns: the No. returns to the same scent source in one session. The contribution of the three factors to the No. F bouts in percentage are given in brackets. Dur: the mean duration in s of all F bouts

Animals		No. obs	No. occ F	N F / No. occ F	No. sc. s	No. rep. F bouts	No. returns	$\overline{\text{Dur}}$
Observation room A Spring 1973 Trial 1								
Jason	♂	9	7	3.3	14 (61)	8 (35)	1 (4)	4.4
Kazan	♂	10	10	3.2	26 (81)	6 (19)	-	3.6
Nico	♂	8	8	3.8	16 (53)	12 (40)	2 (7)	4.3
Grietje	♀	14	7	2.1	14 (93)	1 (7)	-	3.7
Isodora	♀	13	11	2.5	20 (69)	8 (28)	1 (3)	4.2
Leonarda	♀	15	12	1.9	21 (91)	1 (1)	1 (1)	3.7
Observation room B Fall 1973 Trial 1								
Kazan	♂	9	7	3.7	17 (65)	7 (27)	2 (8)	3.6
Tinus	♂	9	7	2.9	14 (70)	4 (20)	2 (10)	3.8
Victor	♂	13	12	3.7	22 (50)	14 (32)	8 (18)	2.9
Leonarda	♀	13	11	1.6	17 (100)	-	-	2.4
Odilia	♀	13	12	2.2	15 (57)	10 (39)	1 (4)	3.5
Observation room A Spring 1973 Trial 2								
Jason	♂	15	10	1.7	10 (59)	7 (41)	-	4.4
Kazan	♂	16	8	2.1	8 (47)	8 (47)	1 (6)	3.5
Nico	♂	13	8	2.4	8 (44)	10 (53)	1 (3)	4.3
Grietje	♀	14	7	2.1	9 (60)	6 (40)	-	3.8
Isodora	♀	14	9	1.0	9 (100)	-	-	4.5
Leonarda	♀	15	5	1.0	5 (100)	-	-	1.6

Trial 1: Under these conditions ♂♂ exhibit F more frequently than ♀♀ do (Tables 1 and 2). Three factors may underlie this phenomenon: 1) the number of scent sources explored by the animals releasing F; 2) the number of F bouts per pattern (indicating the intensity of the attention for this particular smell); the number of times an animal returns after a while to the same scent source.

Table 1 shows that all three factors do influence the frequency of F in most of the animals, but that the number of scent sources is the most predominant one, whereas returns to the same scent source occur very rarely. It seems clear that all three factors contribute to the increase of F in ♂♂ as compared to ♀♀.

Trial 2: Besides the semi open-field situation we compared the results of trial 2, where, as mentioned in Material and Methods, the test-situation is different: the scent source is, at the end of trial 1, presented by the observer; the cat reacts by approach and exploring. If F (or other reactions) follow, some-

times in a long series and next the animal walks away, the trial is closed. The first and third factors are thus excluded in this way.

The frequency of F in trial 2 of the ♀♀ in this situation appears not to be different from that of ♂♂ (Table 2).

Table 2: Mean Frequency ($\overline{\text{Freq}}$) and mean Duration ($\overline{\text{Dur}}$) of Flehmen (F) of each ♀ as compared with each of the tomcats in the same test situation (observation room A or B). +: Freq (resp. Dur) of one cat is lower (resp. shorter) than that of one of the tomcats (sign test). The data from the two observation rooms for trial 1 were pooled

	No. obs.	+	P value
$\overline{\text{Freq}}$ F	trial 1	15	<.01
	trial 2	9	n. s.
$\overline{\text{Dur}}$ F	trial 1	11	n. s.
	trial 2	6	n. s.

Habituation. — It happens regularly that a cat during exploration of the observation room, returns to a scent source which it investigated a few min before. The interest exhibited by the animals in the same scent source after a first, second, sometimes even more returns, appears to wane. We consider this phenomenon as a habituation process. It also happens that an animal sniffs at several scent sources before it returns to the first one.

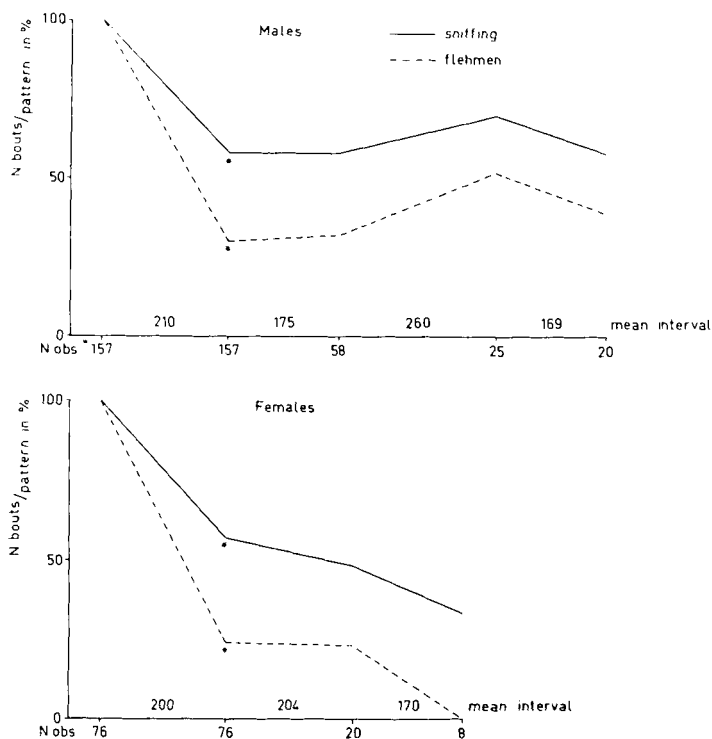


Fig. 5: Habituation of Sniffing (S) and Flehmen (F) patterns of the same scent source. Abscissa: The mean intervals as "estimated by" the animals, between the consecutive S patterns and the same stimulus; N obs.: Number of observations. Ordinate: N of bouts per pattern related to that of the first S resp. F patterns. For significant decrease of the Frequency (Freq) of S and F bouts between first and second or subsequent "self stimulation" indicates $P < .05$ (sign test)

This might lead to a habituation process similar to crosshabituation. We found, however, no indication for mutual interference of the sequential S-F patterns to different scent sources (sign test). This phenomenon is expressed in the duration of the S and F patterns, which was published earlier (VERBERNE et al. 1974) and in the frequency of the S and F bouts per S-F pattern, which will be presented now. The results are given in Fig. 5 for 12 ♀♀ and 9 ♂♂.

The No. of observations and the mean intervals (estimated by the animals) between successive patterns are given on the abscissa; it can be stated in general (cf. also Figs. 7 and 3) that the mean intervals vary, but do not show a clear trend during the sequential returns. The mean number of S and F bouts related to that of the first S-F patterns is presented on the ordinate. The picture shows that the frequencies of both S and F bouts decline during repetitive stimulation, but the slopes for S and F are different (χ^2 test, $P < .01$). Both behaviours S and F show a tendency to recover after the second return for the ♂♂ only.

3.2. Reactions to rubbed and rolled spots. — The most common reactions to rubbed spots are S and Ru. F is a very uncommon reaction.

3.2.1. S rubbed pegs. — A rubbed and a clean peg were presented during the observations. A rubbed peg evoked a longer mean duration of S than a clean peg in all 13 animals (Table 3). 8 animals out of this group have a significant preference for the rubbed peg, as shown by the No. of observations where the mean duration of S a rubbed peg exceeds that of S a clean peg (sign test).

A complicating factor in this comparison could be introduced in the case that a cat, roaming around, perceives the scent of a rubbed peg by air and consequently is more frequently attracted by the rubbed peg. Therefore we

Table 3: Comparison of Duration (Dur) and Frequency (Freq) of Sniffing (S) at a clean and a rubbed peg. No. obs: number of observations of each animal, i. e. No. visits when allowed to explore the observation room; No. occ +: No. occurrences where the animal sniffs at the rubbed peg (Ru peg); No. occ -: No. occurrences where the animal sniffs the clean peg (Cl peg); Dur of S: the mean duration of S a Cl or a Ru peg; +: No. obs where Dur S a Ru peg is longer than Dur of S a Cl peg during one observation; -: No. obs where Dur of S a Cl peg is longer than Dur of S a Ru peg; Dur of the first S pattern: Dur of the first olfactory exploration only; Dur in s: Dur of the first olfactory exploration in seconds; Freq of S: the mean Freq of exploration/observation. Data from animals performing less than 5 occ have been omitted; further details in text. The No. occ underlying the mean Freq of S is lower than that of the first pattern because occ, where Ru occurred, had to be rejected. P after sign test

Animals	No. obs	No. occ +	No. occ -	Dur of S			Dur of first S			Dur in s		Freq of S	
				+	-	P	+	-	P	+	-	+	-
Bartje ♂	17	14	13	10	1	<.02	7	4	n. s.	2.74	1.92	1.86	1.31
Kazan ♂	34	28	28	20	5	<.01	18	7	<.05	5.26	2.96	1.21	1.18
Nico ♂	31	21	21	12	2	<.02	11	3	<.05	4.38	3.13	1.52	1.24
Quintus ♂	30	28	28	16	10	n. s.	19	7	<.05	5.41	2.89	2.43	2.21
Victor ♂	57	43	40	28	5	<.01	25	8	<.01	4.87	1.88	2.27	1.39
Wouter ♂	20	17	16	9	6	n. s.	11	4	n. s.	4.49	2.33	2.00	1.88
Elizabeth ♀	49	17	18	13	2	<.02	11	4	n. s.	4.44	2.00	1.34	1.21
Grietje ♀	44	22	23	22	8	= .02	12	11	n. s.	5.90	4.40	2.00	2.00
Isodora ♀	33	10	9	1	1	n. s.	0	2	n. s.	3.02	2.68	1.10	1.00
Leonarda ♀	57	43	39	29	6	<.01	29	6	<.01	4.76	2.25	1.37	1.37
Odilia ♀	57	40	37	25	7	<.01	25	7	<.01	3.96	1.79	2.23	1.45
Persephone ♀	35	16	17	8	5	n. s.	7	2	n. s.	4.29	3.02	1.33	1.22
Raja ♀	35	23	24	11	9	n. s.	14	7	n. s.	4.09	2.36	2.29	2.52

compared the No. of observations where the rubbed peg was explored "No. obs. +" against the "No. obs. -" where the clean peg was found and investigated. It appeared that the differences can be neglected (Table 3). Moreover these differences are excluded when using the sign test for paired variables, thus in case both pegs have been sniffed.

The exploration of the pegs (clean or rubbed) was followed by Ru in some animals. This might influence the "information-value" of the peg as the original scent was, at least partly, covered by the scent of the exploring cat. Therefore we also compared the duration of S of only the first time a cat sniffed a peg. Comparing the first S duration with the mean S duration we found about the same results (Table 3).

The mean frequency of S (cf. legends of Table 3) given on the right side of Table 3, indicates that a rubbed peg will also be explored more frequently than a clean peg (sign test, $P < .05$). Sexual differences in reactions could not be stated, neither in their ability to discriminate between clean and rubbed pegs, nor in duration or frequency of the S patterns (Mann Whitney U-test).

3.2.2. Sniffing rubbed objects. — Three particular places in the observation room were preferentially rubbed by a number of visitors, both ♂♂ and ♀♀. These places were the two side-rims of the trunk (cf. Fig. 3) and a beam near the door. There were other favourite places like the upper rim of the trunk, but the precise location was too inexact for the observer, so that these places were excluded. Due to our test procedure in an open-field situation, namely visits of a number of animals consecutively on one day, the chance that one of the favourite places would be rubbed by ♂♂ as well as by ♀♀ increases during the successive observations. We checked for the male and female receivers that got sufficient occasions to discriminate between objects rubbed by ♂♂ and those rubbed by ♀♀, whether they are able to discriminate between them. This appeared not to be the case, neither for the ♀♀ ($N_1 = 32$, $N_2 = 26$) nor for the ♂♂ ($N_1 = 44$, $N_2 = 35$) as reflected in the duration of the first S patterns (Mann Whitney U-test).

The results are presented in Table 4. The data for the three particular objects are presented together for each of the animals. The sign test, however, was applied to the mean duration of S or mean frequency of S concerning each object, when these were either not rubbed or had just been rubbed by the pre-

Table 4: Comparison of mean Duration (\overline{Dur}) and Frequency (\overline{Freq}) of Sniffing (S) at three clean or rubbed objects in the observation room. Abbreviations as in Table 3

Animals	No. obs	\overline{Dur} of First S				\overline{Freq} of S			
		No. occ +	Ru	No. occ -	Cl	No. occ +	Ru	No. occ -	Cl
Bartje ♂	6	9	4.2	1	1.9	8	1.7	1	3.0
Kazan ♂	29	42	5.0	9	3.8	31	1.5	7	1.0
Nico ♂	22	28	3.9	12	4.1	18	1.1	11	1.2
Quintus ♂	26	38	3.1	7	2.2	11	1.4	1	1.0
Victor ♂	57	48	5.5	53	3.5	42	2.0	41	1.6
Wouter ♂	16	28	2.8	6	4.3	4	1.3	2	1.0
Elizabeth ♀	36	34	6.8	15	3.4	30	2.1	15	1.8
Grietje ♀	22	16	6.2	10	3.2	15	2.3	9	1.8
Isodora ♀	22	20	8.1	3	3.4	20	1.3	3	1.3
Leonarda ♀	57	19	7.7	63	4.8	19	1.5	63	1.2
Odilia ♀	57	15	5.0	73	3.4	8	2.8	59	1.8
Persephone ♀	35	20	8.0	13	4.8	20	2.8	13	1.7
Raja ♀	35	30	5.2	14	2.8	30	2.6	14	2.1

ceding animals. It is obvious (Table 4) that each animal spent more time on exploring a rubbed spot than a clean one. Also the frequency of S increased likewise, in other words, the animal returns more frequently to the same object to be reformed about the scent.

Sexual differences: Comparing the duration of S performed by the ♂♂ with that performed by the ♀♀ we find that the ♀♀ explore rubbed objects longer than ♂♂ do (Mann Whitney U-test, $P < .001$); the same applies, but less clearly, to the mean frequency ($P < .10$).

The sign test, applied to the differences in duration and frequency of S on each of the three objects separately, demonstrated that ♀♀ discriminate more precisely than ♂♂ do:

Duration S	♀♀ N=15	$P < .01$;	♂♂ N=12	$P < .10$
Frequency S	♀♀ N=14	$P < .01$;	♂♂ N=11	$P < .10$

3.3. *Rubbing as a reaction on a rubbed spot.*

3.3.1. Ru a peg, either the rubbed or the clean peg, was performed infrequently by the animals or not at all. Only three ♂♂ rubbed both pegs after having sniffed them, during one observation. They did not show any preference in Ru clean or rubbed pegs. The scarcity in Ru the pegs cannot be due to an infrequent exploration of the pegs as can be noticed in Table 3 in which S both pegs is almost equally and amply present.

3.3.2. Although all animals rubbed objects, and most of them rather frequently, none of the ♂♂ or ♀♀ responded differently with Ru after olfactory exploration of the clean as compared with the rubbed objects.

Rolling. — It was in most cases not absolutely clear whether only a particular scent source elicited Ro, or whether a scent carrier, e. g. a particular corner of the observation room with fresh and/or old urine contributed to the release of it. We felt unable, therefore, to analyse Ro as a response to a particular scent source by means of the generally used parameters occurrence, frequency and duration.

Analysis of the S-Ru pattern. — Ru following S scents consists of S-Ru patterns composed of S and Ru bouts only, comparable to the S-F patterns described above. The difference between the two types of patterns is that Ru is a marking act and disturbs the original stimulus situation by mixing foreigners' and their own gland secretion in those cases in which the explored objects have been rubbed previously.

The analysis of the S-Ru patterns was therefore only directed towards possible differences in reactions according to the sex of the exploring animal. Patterns of S-Ru are composed — just as S-F patterns — of a single S and a single Ru bout ("single" pattern) or of more S and/or Ru bouts ("repetitions"). Single patterns occur almost twice as frequently as repetitive patterns in ♀♀ (N = 130, resp. 66) and in ♂♂ (N = 185, resp. 98) for rubbed pegs and objects. We analysed the S-Ru patterns in the same way as the S-F patterns (Fig. 6):

1. During the course of the repetitive S bouts in one pattern Ru appears to decrease similarly in ♂♂ and ♀♀ during the first two repetitions but is somewhat restored in long (up to 8) repetition series in relation to that of S in the same order number of repetition.
2. The mean duration of S decreased after the first bout in the repetitions that followed but already showed a recovery in the second repetition and finally increased beyond the original value, at least in the ♀♀.
3. The analysis of the S-Ru patterns resulted in a second sexual dimorphism:

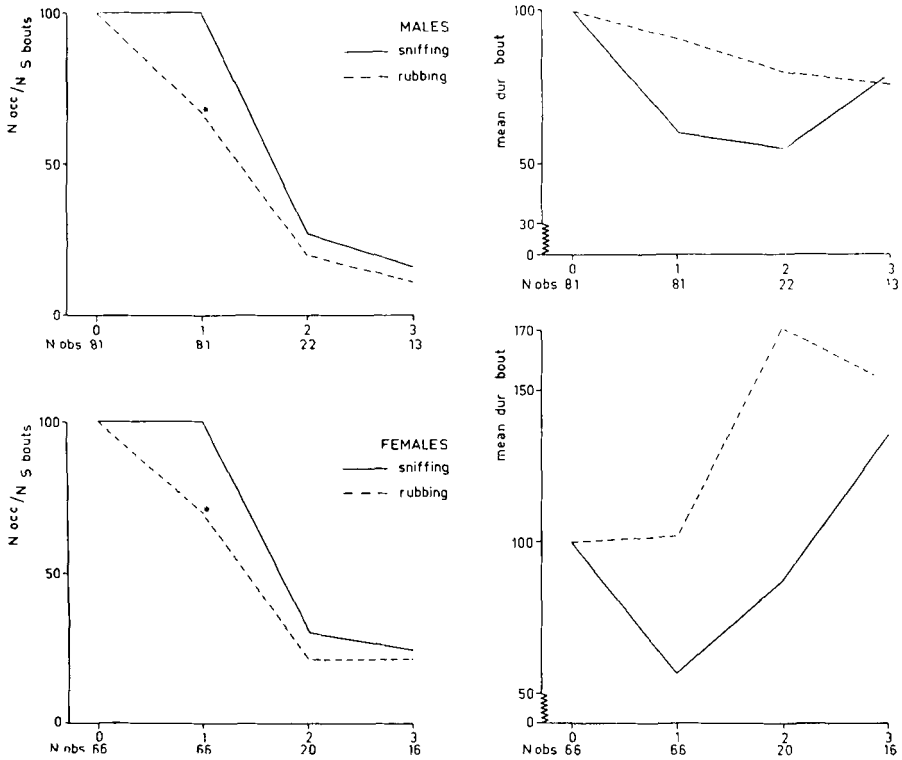


Fig. 6: Data from repetitive Sniffing (S)-Rubbing (Ru) patterns of ♂♂ and ♀♀ on rubbed objects. Left side: Number of occurrences (N occ) divided by N of S per order number. Right side: mean duration of S and Ru related to that of the first bout. Other explanations as in Fig. 4

The duration of Ru was increased in repeated Ru bouts in one pattern in ♀♀, whereas it decreased in ♂♂.

Habituation. — Whereas the habituation of S-F patterns was almost completely restricted to reactions to urine, we also investigated the interest of the animals in skin gland secretion during repeated self stimulation in the same way. We have to keep in mind here, just as in S-F (see above) and S-Ru patterns, that S on the one hand “produces” and presents the stimulus to the sensory epithelium, whereas on the other hand a longer S, e. g. on a rubbed peg must be interpreted as a response to the scent which is based on a positive feedback process. The only parameter in this case is the duration of S, but, on the other hand, the test situation with rubbed and clean pegs gave us the opportunity to discriminate between the effects of habituation and reiteration of a simple orienting S clean objects versus that of S marked places. As soon as the receiver responded to this exploration with Ru the scent carrier, we terminated the series of S patterns. Returning to pegs sniffed beforehand led to a decrease of S duration in both series. The course of the diminution of the response was longer when the animals sniffed rubbed pegs than when they sniffed clean ones, also the slope was steeper. Both features were apparent in ♂♂ and ♀♀ (Fig. 7).

The last variable susceptible to habituation that we investigated were the S-Ru patterns. The duration of Ru consisted either of one bout of long and

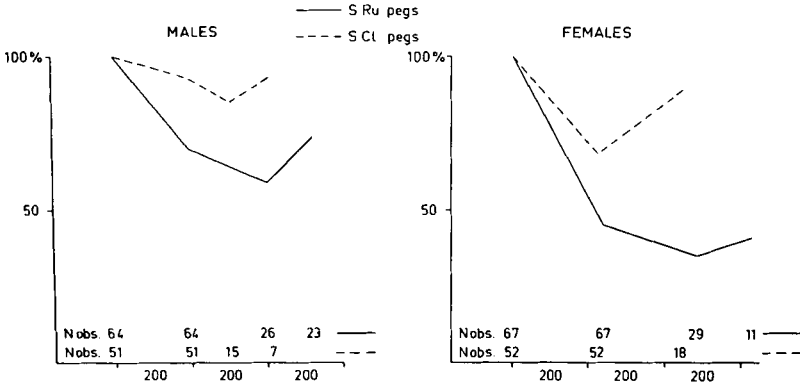


Fig. 7: Habituation of Sniffing (S) with regard to rubbed and clean pegs. Ordinate: Upper row: Number of observations (N obs.) of S rubbed pegs; middle row: N obs. S clean pegs; lower row: Intervals in s. Abscissa: Mean duration of S per bout related to that of the first bout. For further explanation see text

uninterrupted movements of the head and cheeks, or the summated duration of a number of separate successive strokes. Analysis was done in the same way as the S-F patterns. Both the number and duration of S and Ru bouts with regard to objects in the observation room declined in ♂♂ (Fig. 8); the occurrence of S and Ru bouts showed a recovery in the third return, just as the duration of Ru, whereas the duration of S decreased gradually during reiterating self stimulation. The duration of Ru in ♀♀ showed the reverse: it increased gradually (Fig. 8), whereas the preceding S duration decreased and did not

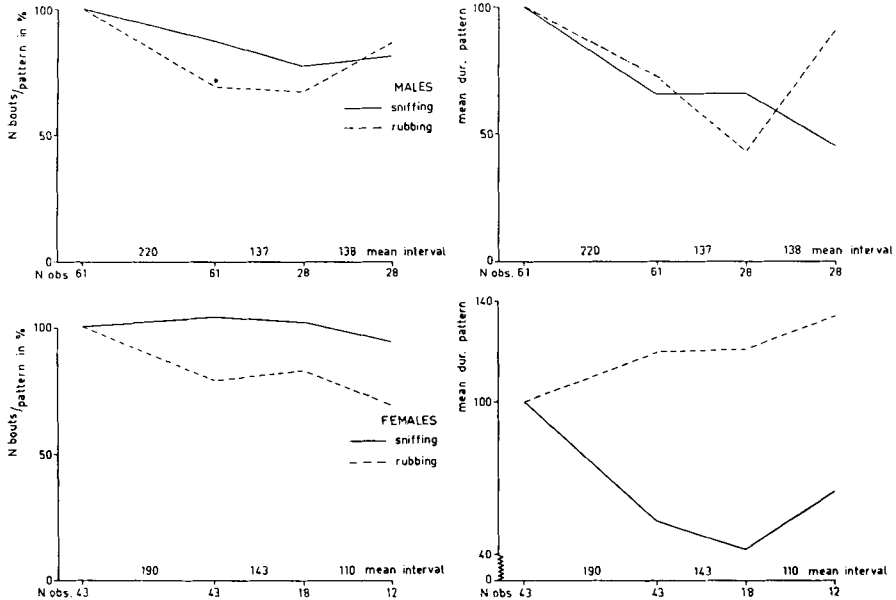


Fig. 8: Habituation of Sniffing (S) and Rubbing (Ru) with regard to rubbed objects. Left side: number of bouts per pattern related to that of the first pattern. Right side: mean duration of S resp. Ru related to that of the first bout. Other explanations as in Fig. 5

show a recovery until the third return. The number of S bouts remained fairly constant while that of Ru decreased.

Summarising we can conclude that both S and Ru on objects are susceptible to repeated stimulation, but respond to a great extent independently of each other.

4. Conflicting reactions after S scents

A variety of reactions can be expected after S scents such as urine or skin gland secretion, as has been described above. To sum up: F, calling, Ru, Ro and attempts to bury the scent.

S urine is usually followed by F; attempts to bury followed only immediately after having produced the urine. In this particular reaction F was the second reaction in sequence after S, but in all other situations F was the dominant and first reaction following S, when e.g. both F and Ru were evoked or F and Li. Some cats called in between the S-F patterns.

A reaction, especially competing with Ru after S a rim or a beam, is scratching with the forepaws. We were unable to attain any evidence for a possible marking function of this behaviour. Most of the cats never performed Ru after S urine. There were, however, individual differences; some tomcats developed Ru, and in a second stage Ro. In a few cases urine evoked Li only: they did this often on dried urine, probably intended here to take up some salts. When the urine was wet they did it preferentially and very carefully along the rim of the spot where urine had dried up earlier.

The physical characteristics of the *scent carrier* seemed to play a secondary role, but it appeared that urine sprayed out on a beam more frequently evoked Ru than on a flat wall and that urine on the floor released more Ro than on a vertical object. Cotton-wool evoked playing and chewing in some cats in between the real reactions to the scent, whereas a peg with urine on top could cause Ru. As already demonstrated in 3.3., cats prefer to rub rims of a trunk or a beam rather than the round tip of a peg. Nevertheless a cat very rarely rubbed an object without olfactory inspection. In a more social context the cat rubbed with its side along the beam without S beforehand, when it looked and called to the observer. The same happened sometimes when the observer entered the observation room.

We also refer here to p. 88 about the readiness of a female cat to rub a peg when the observer presented it, whereas, on the other hand, the same cat never rubbed a peg during olfactory exploration.

5. Sexual pheromones in urine and skin gland secretion

An estrous cat, as is generally known, is especially motivated to rub and roll during this period (LEYHAUSEN 1973 a, MICHAEL 1973) and, although rather seldom, to spray or to urinate somewhere in the room without making attempts to bury the urine. In both cases the behaviour seems to serve chemocommunication as the chance for the tomcat to find her on the basis of olfactory cues is enhanced. A second factor could be the change in chemical substances, metabolites of estrogen in urine and vaginal or perigenital secretion as is shown in other mammals (MICHAEL 1973, WHITTEN and CHAMPLIN 1973) or change in the size of sebaceous glands (MONTAGNA 1963). For this purpose we set up another experiment in which the female donor of the cheek gland secretion on the "rubbed peg" also served as a donor for urine. We observed

the interest of other animals in her cheek gland secretion, presented in trial 1 and her urine in trial 2, and plotted the interest of the ♂♂ and ♀♀ as a function of time. In the time epoch we used, she showed behavioural indications of several estrous cycles. The interest in urine was measured by the frequency of F bouts, that of cheek gland secretion by the duration of the first S pattern on the rubbed peg divided by the S duration on the clean peg. The reason for using this ratio was to minimize possible fluctuations in the S motivation of the receivers. The mean frequency of F bouts averaged over tomcats and cats are given in Fig. 9.

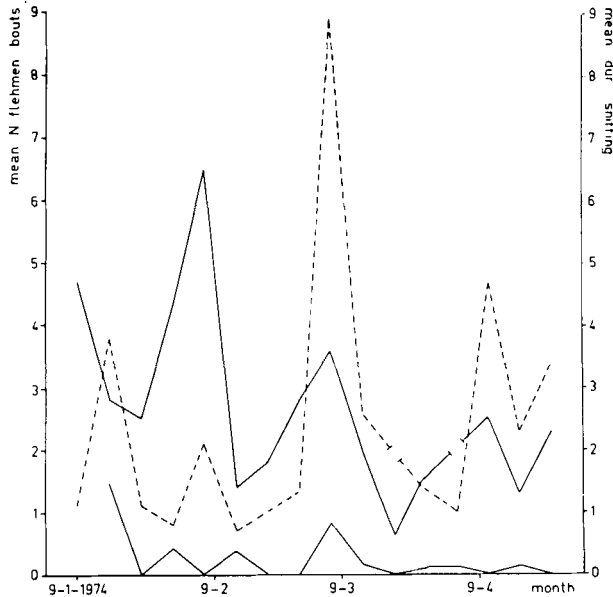


Fig. 9: Oscillating interest of 5 tomcats, as represented by the mean number of Flehmen (F) bouts after Sniffing (S) urine of a female cat (left-hand ordinate). The scent was presented weekly over a period of three months (abscissa). The sequence of the ratio duration of S pegs rubbed by the same ♀ to that of the clean pegs, performed by the same tomcats, also follows this oscillation (right-hand ordinate). The Frequency (Freq) of F displayed by the ♀♀ is much lower and follows only two high peaks in the curve of the ♂♂. —: Flehmen bouts of the ♂♂ (upper line); Flehmen bouts of the ♀♀ (lower line); ----: Sniffing the pegs by the ♂♂. Further details in text

It is clear that the interest of the ♂♂ in urine and cheek gland secretion shows a cyclic course. This could not be due to a supposed synchronised oscillating motivation of the ♂♂ to perform F, as the frequency of F evoked by the several scent sources explored during trial 1 does not coincide with the interest in the two female scents. Pair-pair comparisons between N-F bouts after S urine in trial 1 with that released by Isodora's urine in trial 2 gave a low value, but those between Isodora's urine and the S duration of her cheek gland secretion gave a significant agreement (sign test, $P < .02$), indicating a synchronised fluctuation in the production of interesting scents.

The ♀♀' interest in the urine of Isodora was very low during the course of this experiment as expressed in the frequency of F-bouts, but two small peaks appeared on dates where the tomcats showed a high number of F-bouts.

The mean ratio of the first S pattern of the ♀♀ on the rubbed peg to that of the clean peg followed the cycles shown by the tomcats exactly during the

first 8 weeks, but desynchronised afterwards. Another reaction to urine which caused such high frequencies of F was *calling*. Victor usually called quite often when he found something interesting, but in this case his calling had a lower pitch; also 3 other tomcats called more frequently. This characteristic deep calling showed an equally rhythmic course (sign test $P < .05$). Another characteristic behaviour of tomcats was sitting down near the scent after having flehmed repeatedly, and after a period of "recovery", starting again with S and F. The same behaviour was described earlier for a tomcat in a comparable situation, he finally exhibited F 26 times in 20 min (VERBERNE 1970).

A second opportunity — by chance — was provided by another ♀ "Odilia". She sprayed and urinated once in the observation room within a time period of two weeks. In this situation we compared the frequency of F after S on her own urine with that of S urine of a tomcat, presented in the subsequent trial 2, or, if possible, the urine which was sprayed by one of the tomcats on that particular day (see Table 5).

Table 5: Frequency (Freq) of Flehmen (F) after Sniffing (S) urine of the ♀ "Odilia" (A), which she had just sprayed or produced from squatting position in the observation room, compared with (B) fresh urine of a tomcat "Kazan"

Animals	A		B	
	No. obs	Freq F	No. obs	Freq F
Nico ♂	1	3.0	1	1.0
Quintus ♂	1	7.0	1	3.0
Victor ♂	2	13.0	2	2.2
Wouter ♂	2	6.5	2	3.0
Leonarda ♀	1	2.0	1	0.0
Odilia ♀	2	0.0	2	0.5

All animals — except the donor — showed a higher number of F bouts on her urine than on the comparably fresh urine of the tomcat. Another interesting reaction was performed by two tomcats. They squirted after exploration of her marking altogether 3 times.

Discussion

In our research to establish the existence and, in a second stage, the function of urine and skin gland secretion of cats as pheromone carriers, we approached this question along three lines. 1) The performance of "marking" acts, i. e. spraying urine and Ru/Ro. The validity of using the term "marking" depends on: 2) The reaction of the animals exploring spots which were sprayed or rubbed. 3) The differences in both marking and behavioural reactions in the two sexes to the same scent stimulus.

The most important variables used in this study were: S, F, Ru/Ro. A variable to be considered as one of the "second dimension" was the occurrence of habituation processes.

We will start discussing the latter first because habituation is an intrinsic part of the explorative behaviour in a semi open-field situation, so that the observer must consider the successive events during the course of time with caution.

Exploratory behaviour and habituation

Habituation is generally considered as a decrement of a response, behavioural or neurophysiological, to repeated stimulation; the stimulus is presented by the investigator usually at fixed intervals.

The present study is involved with four aspects of repeated stimulation.

1) We "stimulated" the animals once a week by releasing them in the observation room for 15 min; the response was measured in the frequency and duration of a sequence of behavioural acts, which have been divided in four main categories: Explorative behaviour, Rest and Grooming, Ru and Ro and finally F. We checked whether any of the four categories showed a tendency to decrease or increase during the first 10 weeks, but found none.

2) The release of cats and tomcats in the observation room (in fact conforming to a semi open-field situation) gave the animals the opportunity to stimulate themselves by visual and olfactory exploration during a time period of 15 min in trial 1. Olfactory exploration and F declined gradually (substituted by Comfort and Rest) (Fig. 2).

This phenomenon seems to us to be based on habituation, namely that of the "novelty" or "curiosity" response.

Our results confirm those of GLICKMAN and VAN LAER (1964), who observed reactivity of several cat species to novel objects in a stimulus situation comparable to ours.

Ru and Ro did not show any organised time-dependent tendency. It seems as if two conflicting factors underlie this phenomenon:

- a) An original inhibition of S-Ru by explorative motivations. Earlier we pointed (cf. Chap. 4) to the fact that F is dominant over Ru when both reactions are evoked by the same stimulus. Another argument supporting this contention is the shift of Ru and Ro from the second and third epoch of 5 min to the first one when the occurrence of F is decreased tremendously by closing the vomeronasal duct (cf. part II).
- b) An arousal by the stimuli, which are successively explored (see also below under 3). Moreover, the performance of Ro and Ru by ♀♀ seems to be dependent not so much on the environment but rather on the hormonal state of the animal (LEYHAUSEN 1973 a, MICHAEL 1973).

3) During returns to the same scent source in the observation period of 15 min, the "intertrial-interval" is estimated by the animal itself. The advantage of this type of sequential stimulation is that a possible decline of the orienting ("novelty") response (VOSSEN 1966) does not interfere with the habituation process proper. The reactions connected with this type of stimulation were S, S-F and S-Ru patterns; No. and duration of bouts per pattern were used as parameters. All variables tested appeared to be susceptible to repeated stimulation by showing decrement, followed by recovery.

The combination of these two features underlines the validity of considering the fluctuations as a habituation process (THORPE 1963, HORN and HINDE 1970, PEEKE and HERZ 1973). There is, however, one exception to the rule given: The duration of Ru in ♀♀ is susceptible to repeated stimulation in a reverse sense: it increased, even where the preceding olfactory inquiries were made in a shorter time period. This feature suggests rather a kind of self-reinforcement, based on a positive feedback. In this respect we refer to KIMMEL (1973), who points out that especially Grooming — or sexual stimulation — mainly enhances afferent input to the central nervous system. In this sense Ru could be considered as a kind of stimulation. Also LEYHAUSEN (1973 b)

observed in several felids that Ru and Ro occur at least partly independent of olfactory stimulation. He considers this behaviour, as well as F, as a kind of addictive behaviour. Indeed, also our cats sometimes seemed unable to stop Ru and Ro after having got in the right mood.

4. S-F or S-Ru patterns are the smallest units organised and used for information retrieval by our animals.

Repetitive occurrence of S-F bouts, resp. S-Ru bouts in one pattern could in fact also be considered as "massed trials" (PEEKE and HERZ 1973) where in this particular case the No. of S is equal to the No. of scent stimuli, which may evoke two types of reactions: a longer duration of S and the occurrence of F and Ru. Both types of reactions appeared to habituate with 2 exceptions: a) The duration of F does not change in the successive bouts in one pattern. The implications of the latter part will be raised in part II. b) ♀♀ increase their Ru activities during consecutive patterns, whereas the time spent on preceding information does not predict this.

The other side of the significance of such an organised unit as an S-F and S-Ru pattern is that the use of repetitive S suggests that the olfactory information has to be renewed in order to lengthen the appropriate reaction. This holds for F as well as for Ru. Therefore we consider the length of the pattern or the No. of S and F resp. Ru-bouts as a parameter of the intensity of the animals' reaction.

Pheromones

1. *Urine*. — On the basis of our observations it is clear that our tomcats showed a cyclic intensity of interest in the ♀'s urine over the course of 3 months, which is represented in the frequency of F (Fig. 9).

In another case (Table 5) both cats and tomcats showed unusual high F frequencies on urine of an apparently estrous ♀ that deposited her urine in the observation room. These data confirm earlier results on a tomcat and some other small Carnivora (VERBERNE 1970) and those of a lion (EATON 1974). SCHNEIDER (1932) mentions that F as displayed by the big Felidae occurs especially during sexual play and copulation. BANKS (1964) denies that F has this "olfacto-sexual response enhancing the male's ability to detect an estrous female" (ewe), but FRASER (1968) stated that male ungulates in general show more F to urine of ♀♀ in heat and TOMKINS and BRYANT (1974) demonstrated this for the ram in particular. Further support comes from the giraffe (DAGG and TAUB 1970).

SHANK (1972) observing male feral goats, found that F on female urine, in about 95 % of the cases inhibited further "sexual pattern". He concludes that F is an effective means to establish the non-estrous condition of the ♀ in these cases.

None of the authors (except the last), however, support their statements with quantitative data.

SCHALLER (1967) reported that the male cheetah, after having flehmed the urine of an estrous ♀ follows her. He also found in the Ungulates and in the gaur that dominant sexually active ♂♂ perform more F and also mount and copulate more frequently than the other ♂♂. The higher occurrence of F seems to depend on the better opportunities of dominant ♂♂ in these circumstances.

If F is utilised by mammalian ♂♂ in estimating the hormonal state of the queens, what then would be the function in ♀♀? Although our female cats perform it somewhat less frequently (see Table 1 and Fig. 4) most of them do

it quite readily and in a way indistinguishable from that of ♂♂. The other purpose to employ F might be to sample information from fresh and old urine which plays an important role in territorial relation (DE BOER in prep. 1, EATON 1974, LEYHAUSEN and WOLFF 1959, SCHALLER 1967).

It is not clear whether this sexual pheromone is part of the urine and/or is produced by vaginal tissue, resp. perigenital skin glands. LYDELL and DOTY (1972) found that male rats preferred estrous urine odour to diestrous urine both obtained from externally voided urine (possibly mixed with vaginal secretion) and also preferred that obtained directly from the bladder. But HAYASHI and KIMURA (1974) showed that male mice did not prefer urine, but only vaginal smears from estrous ♀♀. The vaginal secretion in monkeys also contains a sexually stimulating factor, but urine was not investigated in this case (MICHAEL 1973). We were unable to find any data on the cats in the present literature available.

The simultaneous fluctuation in giving deep calls by some tomcats is an additional but interesting response to a pheromone carrier. It reminds us of the original solitary life of the wild cats, which would have used it in an attempt to find each other at the appropriate moment, for mating and fertilisation. Also EWER (1973) points to "mating calls" which help the ♂♂ to locate the ♀.

Arguments for the role of urine in chemocommunication between tomcats in a social or territorial context will be published elsewhere (DE BOER in prep. 1) but it can be pointed out here that dominant tomcats spray urine more frequently than subordinate animals. A second interesting finding in this respect is that tomcats hardly ever put their urine mark on that of other preceding visitors (DE BOER in prep. 1).

2. *Skin gland secretion.* — Cats rub and roll parts of their body where according to SCHAFFER (1940) sebaceous glands are well developed. The result of our study contributed to the concept of chemocommunication among cats by means of these glands, especially the cheek glands.

1) The longer S duration of rubbed pegs and particularly favourite objects in the observation room. The fact that the pegs were rubbed by one of the ♀♀ as a greeting does not give rise to doubt as to the release of pheromones by Ru, especially as the rubbed objects marked by solitary exploring animals after S in the observation room released similar reactions.

Moreover:

2) The tomcats showed oscillating interest in the female skin gland secretion on the pegs, strongly time-related with their interest in her urine. The time-characteristics of this oscillation suggest a reflection of her estrous cycle (Fig. 9). The low intensity of Ru her cheek on the peg with closed mouth rules out the possibility of saliva being a pheromone carrier, as suggested by BOUDREAU and TSUCHITANI (1973).

Although we could not check with exactitude the amount of secretion which Isodora left on the peg weekly, we have, for some reason, no ground to ascribe the different reactions of the tomcats to the difference in quantity of rubbed secretion. To our knowledge there is no other finding in mammals concerning a skin gland carrying sexual pheromones (we are excluding here glands opening into anal or urogenital tracts). The size and activity of sebaceous glands is according to MONTAGNA (1963) partly controlled by gonadal secretion. THIESSEN and LINDSEY (1970) however, found no effect of estrogen and progesteron on the marking activity with ventrally sebaceous glands in mongolian gerbils. OWEN and THIESSEN (1974) found later marking activity in the

same species to be dependent on the amount of estradiol benzoate, but only in combination with progesteron. They did not investigate the interest of ♂♂ in the secretion of ♀♀ depending on their sexual state.

Also GOODRICH and MYKYTOWICZ (1972) found sexual differences in several compounds of the secretion after analysing secretions of chin, anal and inguinal glands of rabbits, but did not observe possible differences in reactions on these scents.

3) ♀♀ discriminate better between clean and rubbed objects than ♂♂ do in our test situation. They also spend more time on exploring the scent. These data agree very well with LEYHAUSEN's statement (1971) that ♀♀ are more "territorial-minded" than ♂♂ are.

4) The interest in rubbed pegs showed a rapid decrease after repetitive self-stimulation as compared with the interest in clean pegs (Fig. 7). The probable explanation is that the original and long duration of S achieved by a positive feedback as a result of the interesting scent on the rubbed peg, is shortened during the returns by a process of habituation and recognition, whereas the exploration of the clean peg at the first time of S was almost at a minimum level and served only as an attempt to find out if there were some scent worthwhile to spend more time or not. But even this orienting S appeared sensitive to a learning process.

5) ♂♂ do not rub more frequently than ♀♀ do. This finding is not in accordance with that of studies on other mammals.

Scent marking is, as a rule, androgen dependent (cf. reviews of GLEASON and REYNIERSE 1969 and HART 1974).

Considering our preliminary results — attained under somewhat different circumstances (DE BOER et al. 1973) — it was amazing to discover in this study a complete lack of evidence for the ♂♂' abilities to discriminate between clean and rubbed pegs by means of Ru responses after olfactory exploration, irrespective of the sex of the donor. One could imagine that skin gland secretion of ♀♀ only participates in sexual communication, so that Ru and Ro responses of the receiver on the same spot seem rather senseless, if not disturbing.

In a social context, however, it could be that the next visitor to the territory puts its fresh mark on that of the predecessor. In the present situation this appeared not to be the case: none of the ♂♂ or ♀♀ responded differently with Ru pegs and objects rubbed either by ♂♂ and/or ♀♀, despite the fact that both sexes were able to discriminate between clean and rubbed objects, as mirrored in the differences in S duration. Neither, for the same reason, is there any doubt that the Ru act does not leave any scent.

In contradistinction to this partial lack of evidence for the role of skin gland secretion in social (i. e. non-sexual) communication we found that dominant tomcats rubbed more frequently both during the encounters and as single exploring visitors (DE BOER in prep. 2). Summarizing we may conclude that the smell of other urine or cheek gland secretion does not evoke, either in male or in female cats, attempts to cover this scent with their own, at least in our test situation. If there is any evidence of a tendency to cover strange scents it could be the Ro and Ru activities which are evoked now and then by urine in some of the tomcats.

This phenomenon might be connected with the fact that cats are (or have always been considered as) solitary mammals. Each individual marking has its sense and significance and can function in a common territory, which is divided in time (LEYHAUSEN and WOLFF 1959). This explanation, however, is based

on the assumption that the animals "consider" the observation room as a joint territory. Another explanation could be that marking is also used for "self-assurance" (EWER 1973). There were indeed tomcats that covered their own scent mark every week but not that of others.

Acknowledgements

We thank Prof. Dr. A. PUNT and Dr. P. BLACK-CLEWORTH for their critical reading of the manuscript. We are indebted to our students S. DE JONGE, I. VAN GESTEL and P. OUD for their devoted attention in observing their cats.

Summary

1) A number of domestic cats was observed in a semi open-field situation where scent stimuli of different origin were emitted by the animals.

2) ♂♂ displayed in comparable test situations more frequent urine spraying and flehmen than ♀♀ after having sniffed at the scent stimuli present.

3) The significance of urine and cheek gland secretion in chemo-communication was investigated. Both types of pheromone carriers appeared to function in social as well as in sexual contexts, as could be concluded from the interest of the exploring animals. The interest was reflected in duration and frequency of response patterns consisting of sniffing separately, sniffing and flehmen bouts and sniffing-rubbing (rolling) bouts.

4) The time characteristics and the intensity of the habituation process in olfactory exploration appeared to differ according to the exploration of either clean or rubbed spots, as well as according to the sex of the responding animal.

Both facts suggest that the habituation process can be used when searching for the existence and function of pheromones in animals.

Zusammenfassung

1) Eine Gruppe von 23 Hauskatzen und -katern wurde in einer freiland-ähnlichen Umgebung beobachtet, in der sie Duftstoffe verschiedener Art und Herkunft absetzten.

2) Unter vergleichbaren Umständen markieren die ♂♂ öfter mit Urin als die ♀♀ und flehmen außerdem öfter, nachdem sie an den vorhandenen Duftmarken geschnuppert haben.

3) Die Bedeutung von Urin und von Wangendrüsensekretion wurde untersucht. Die Befunde weisen darauf hin, daß beide Duftstoffe Informationsträger sind, sowohl in sozialem als auch in sexuellem Zusammenhang. Dies ließ sich aus der Reaktion der schnuppernden Tiere ableiten. Die Reaktion wurde nach Dauer und Frequenz ihrer Einzelmuster ausgewertet, die aus Schnuppern-Flehmen und aus Schnuppern-Reiben oder Wälzen bestehen.

4) Die zeitlichen Eigenschaften und die Intensität der Reizgewöhnung waren verschieden, je nachdem ob die Tiere lange unbenützte oder frische Markierungsstellen untersuchten. Bei dieser afferenten Drosselung stellten sich auch sexuelle Unterschiede heraus. Beide Befunde zeigen, daß Vorstellungen über Reizgewöhnung bei der Untersuchung von Vorkommen und Funktion von Pheromonen angewendet werden können.

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