

EUROPEAN COMMUNITY PREVIEW ARTICLE

TOM-CAT ODOUR AND OTHER PHEROMONES IN FELINE REPRODUCTION

K.P. BLAND

Department of Veterinary Physiology, Royal (Dick) School of Veterinary Studies,
Summerhall, Edinburgh EH9 1QH (Great Britain)

(Accepted 3 May 1979)

ABSTRACT

Bland, K.P., 1979. Tom-cat odour and other pheromones in feline reproduction.
Vet. Sci. Commun., 3: 125-136.

The function and suppression of urine 'spraying' by cats is discussed as also is the source of tom-cat odour. It seems unlikely that tom-cat odour is derived from the lipid in the proximal convoluted tubule of the kidney, however its production by the anal glands has not yet been proven. Although male cats show a flehmen response when sniffing urine, smell seems to play a more important role in reproduction in the female than the male. The available data suggests that valeric acid may function as a female/female pheromone in cats by inducing or facilitating oestrus. Nepetalactone, the active ingredient of catnip, is probably not related to any naturally occurring pheromone in the cat but simply acts as an hallucinogenic drug.

INTRODUCTION

This review is an attempt to bring together the available information and indications on the role of olfaction in feline reproduction. For convenience of reference the information is divided into sections.

URINE SPRAYING

Domestic cats of either sex, but particularly males, will "spray" their urine against conspicuous objects such as posts, shrubs and walls (Fox, 1975); in London Zoo the lions seem to delight in using the bars of their cage, much to the anguish of the onlooking crowd. In the male cat this action is accomplished by backing up to the object, twitching the vertically held tail and then "spraying". The term "spraying" has been retained here due to popular usage - it is in fact a misnomer for in the male the urine is not sprayed in a fine mist, but ejected in a forceful short stream. In the female, the spray is more diffuse (McDougal, 1977). This "spraying" by the backward directing of urine by the male occurs in the domestic cat, serval, ocelot, lion, tiger, leopard and cheetah (Fiedler, 1957; Schaller, 1967;

Eaton, 1970), and so seems to be a characteristic of felids, although Fiedler (1957) reports that he never observed captive pumas urinating otherwise than in a squatting position.

Like leg-cocking in the male dog, the ability to "spray" develops in the domestic cat around puberty. Prepuberal castration usually prevents spraying (Hart, 1973; Hart & Barrett, 1973). Castration at puberty or of the adult tom-cat reduces the tendency to spray primarily because the gross behavioural changes accompanying castration reduce its frequency. However, changes in the environment, such as the introduction of another cat, or even another pet, into the home can cause a re-commencement of "spraying" behaviour both in castrates and in cats that do not usually "spray" (Worden, 1959; Fox, 1965, 1971; Hart, 1975). In domestic cats such a resumption of "spraying" for psychological reasons (urological problems can also cause its onset) can usually be suppressed by the administration of either long-acting progestins or oestrogens (Gerber, Jöchle & Sulman, 1973; Hart, 1974a, 1975; Seidenberg, Kornick and others, 1975; Beaver, 1976).

The primary function of urine "spraying" appears to differ between the sexes. It is commonly accepted that the deposition of tom-cat odour by "spraying" by male felids is a form of territorial marking (Todd, 1963a; Schenkel, 1966; Hart, 1975; McDougal, 1977). However, Michael's observation (Michael & Keverne, 1968) that the smell of an active male can evoke typical oestrous behaviour, including oestral crouch and treading, in oestrous queens should not be forgotten. Likewise, Gowda (1968) observed a tigress in heat lie down in the typical mating posture after smelling the freshly voided urine of a male tiger, while Todd (1963b) found that 2 (one male, one female) out of 4 cats responded to the odour of tom-cat urine but not female cat urine by showing "catnip-like" behaviour (see later). In the female "spraying" is predominantly a feature of the heat period and so probably functions primarily to inform the male of the females condition (McDougal, 1977). However, as territorial threats can sometimes cause commencement of "spraying" in female domestic cats, an element of territorial marking must also be involved.

TOM-CAT ODOUR

Unlike "spraying" behaviour which is not irreversibly suppressed by castration, the distinctive "tom-cat odour" released when "spraying" by the male cat is androgen dependant and disappears within a few days of castration (McCunn, 1953; Joshua, 1965; Burke, 1976). The source of tom-cat odour is still uncertain. Two possible sources have been proposed :-

- i) Kidneys
- ii) Anal glands

Each will be considered in turn :-

i) The Kidneys

Tom-cat odour has been claimed to be due to a "lipid component of the urine" (Short, 1972; Fox, 1975) and certainly the odour does appear to be present in the urine in the bladder (Whitehead, 1971). The urine of the leopard (K.P. Bland, unpublished observations) and tiger (Hewer, Matthews & Malken, 1948) is very rich in fat but this is not restricted to the male animal. It has also long been known that the domestic cat's kidneys contain large amounts of lipid in the cells of the FIRST segment of the proximal convoluted tubules (Vulpian, 1861; Treutlein, Lehmann & Rupell, 1914; Mottram, 1915-16, 1916; Smith, 1920; Henschen, 1923; Millot, 1927; Modell, 1933; Modell & Travell, 1934; Nakamura, 1935; Foote & Grafflin, 1938, Gairns & Morrison, 1949). A similar distribution of lipid droplets also occurs in other felidae such as, tiger, lion, cheetah, ocelot, leopard, jaguar and lynx (Henschen, 1923; Millot, 1927; Hewer et al, 1948). Unlike the felidae, the fat in the kidneys of the canidae is restricted to the SECOND segment of the proximal convoluted tubule (Henschen, 1923; Foote & Grafflin, 1938). In the kitten some fat also occurs in the second segment (Helmy & Hack, 1967).

The demonstration by Mary Lobban (1951, 1955) that the quantity of this renal lipid not only varied with the age of the animal but also with its sex and reproductive state seems to have formed the basis for the idea that the kidneys are the source of tom-cat odour, although Lobban herself makes no suggestion to this end. Her findings are summarized in Table I.

TABLE I.

Variation in renal lipid content of male and female cats in different reproductive states (after Lobban 1951, 1955)

Sex of cat	Reproductive condition	Renal lipid content
FEMALE	Kitten	-
	prepuberal	-
	anoestrus	-
	pro-oestrus	++
	oestrus	++
	dioestrus	+++
	pregnant	++++
MALE	Kitten	-
	sexually active	-
	sexually inactive	+++
	senescent	+++

These coupled with the data in Table II (K.P. Bland, unpublished) on the amount of

lipid present in tom-cat kidneys around puberty, do not support the renal lipid as the source of tom-cat odour.

TABLE II

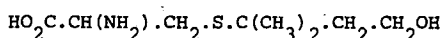
Variation in renal lipid content around puberty in male cats

Wt.of Animal (Kg.)	Whether producing tom-cat odour	Gonadal state		Renal Lipid Content
		Testes descended	Spermatids present	
2.3	No	No	No	-
2.5	No	Yes	No	+ +
2.5	No	Yes	No	+ + +
2.6	No	Yes	No	+ +
2.4	No	Yes	Yes	+ +
2.75	No	Yes	?	+ + +
3.0	No	Yes	Yes	+ + +
3.1	No	Yes	Yes	+ +
3.3	Yes	Yes	Yes	+ +
3.5	?	Yes	Yes	+
3.6	Yes	Yes	Yes	-

Several workers have tried to characterize the lipid in the renal tubule cells. Using histological methods, early workers (Henschen, 1923; Smith & Freeman, 1954) demonstrated the triglyceride nature of the droplets; Smith and Freeman (1954) further found that the distribution of droplets in the renal tubules was correlated with the distribution of lipase and alkaline phosphatase. On the basis of her histochemical work, Lobban (1955) suggested that a significant portion of the tubular lipid may be steroids other than cholesterol and possibly allied to oestrogens. However, acetone extraction and paper chromatography (Helmy & Longley, 1965, 1966) confirmed that triglyceride was the major ingredient, with cholesterol and cholesterol ester also present. No oestrogen could be demonstrated in the extract.

Beta-oxidation of fatty acids from triglyceride breakdown yields ketone bodies (acetone-acetic acid and β -hydroxybutyric acid). Chamberlin, Furgason and Hall (1937) showed that the normal male cat excreted four times more ketones in the urine than did the female; a difference which was abolished by castration but restored again if testosterone propionate was injected into the castrate animal. Could these ketone bodies be responsible for tom-cat odour? Although the odour is wrong, there is certainly something strange about this high ketone excretion for according to Chamberlin et al (1937) the ketone excretion in the tom-cat goes down during fasting, not up as in most species.

A component of the urine of the cats that appears to be unknown outside this family is the amino-acid FELININE:-



First characterized by Westall (1953), this amino-acid is abundant in the urine of the domestic cat, being excreted at the rate of 100-200 mg/100 ml (Westall, 1953; Tallan, Moore & Stein, 1954; Greaves & Scott, 1960). Datta and Harris (1951) showed that 'cat spot', later shown to be felinine, was present in the urine of the domestic cat and ocelot but not in that of the lion, tiger and puma. Although tom-cat odour takes up a characteristic position on chromatographs of cat urine, it is not the same as felinine which is odourless (D.C. Cusworth, personal communication).

ii) The Anal Glands

The anal glands are present in nearly all carnivora; in both the felidae and the canidae they are relatively small (e.g. only 25 mm long in the lion) with the ducts opening on either side of the anus. Their structure is similar in the domestic cat (Greer & Calhoun, 1966), lion (Krölling, 1926; Ewer, 1973) and tiger (Hashimoto, Eguchi & Arakaura, 1963). The nature of their secretions and its function is largely unknown in the felidae although both Krölling (1926) and Greer & Calhoun (1966) have shown their secretions to have both a fatty and an aqueous component. Krölling (1926) and Schaffer (1940) found seasonal fluctuations in the gland's secretory activity; the secretion being most active in the breeding season. In dogs, Donovan (1969) found evidence that the anal glands were concerned with attracting the male to the oestrous female, although the experimental work of Doty and Dunbar (1974a & b) failed to confirm this. The anal gland secretion of the red fox is composed mainly of volatile fatty acids (Albone & Fox, 1971) and one cannot help but recall the similar composition of the pheromone 'copulin' from the vagina of the rhesus monkey (Michael, 1973). Donovan (1969) also suggested an offensive role for the anal glands in the dog; this would be in line with their use in the mustelidae and enhances the suggestion that they may be the source of tom-cat odour.

Surprisingly it is in the largest of the cats, where the distance between the anal glands and the urinary outflow is greatest, that there is the most conviction that anal gland secretions are added to the urine during spraying. Both Schaller (1967, 1972) and McDougal (1977) believe that the lion and the tiger use the urine as a propellant for the anal gland secretions. Certainly in the male lion and tiger the urine jet is often directed upwards at an angle of some 30°-45° (Schaller, 1972; K.P. Bland, personal observations). Neither does a study of the anatomy of the perineal region of the domestic cat refute this idea. The cranial part of the external anal sphincter muscle acts to express the anal sacs as well as acting as an anal sphincter (Martin, Fletcher & Bradley, 1974a). Furthermore, the caudal rectal nerve innervates both the external anal sphincter muscle and the bulbospongiosus muscle in the male cat (Martin, Fletcher & Bradley, 1974b). As early as 1895, Langley and Anderson reported that stimulation of the nerve to the bulbospongiosus muscle of the male cat resulted in the violent ejection of a drop or two of urine from the

penis, and movement of blood to the distal end of the corpus spongiosum penis. Thus it appears that the anal sacs have a common innervation to the structures which are possibly used in spraying.

The dilemma over the source of tom-cat odour may possibly be more apparent than real. It is conceivable that both the urine and the anal sacs contain the odour. Certainly the male cat appears to be able to vary the potency of the odour produced. Also Rosenblatt and Schneirla (1962) observed that when a tom-cat established an area as familiar he sprayed an odorous substance from his anal glands and urinated on the walls and floor!

FLEHMEN AND OLFACTORY LOBES

When a male cat or tiger investigates the urine of another cat, it usually opens its mouth slightly and closes its eyes while sniffing (Verbene, 1970; Fox, 1975; McDougal, 1977); in other species, this FLEHMEN reaction is thought to facilitate the uptake of odour by an accessory olfactory organ, the vomero-nasal organ or Organ of Jacobsen (Estes, 1972). This organ is thought to be associated with the reception of pheromones. Even so the role of true sexual pheromones, as opposed to territorial pheromones, in tom-cats does not seem to be very great for olfactory deprivation (removal of olfactory lobes) of sexually experienced tom-cats does not impede mating (Cooper & Aronson, 1972; Aronson & Cooper, 1974). On the contrary the anosmic sexually experienced male mates more rapidly for the preliminary sniffing behaviour is dispensed with. On the other hand, the small amount of available circumstantial evidence suggests that the situation in the female cat may be quite different. Pheromones may play an important part in facilitating oestrus and mating behaviour.

VALERIC ACID

The root of Valeriana officinalis, Linnaeus or Great Valerian has long been known for its attractiveness to cats (Brown, 1874). In 1805, Boardman warned veterinarians that the root is often contaminated with cat urine, due to this attractiveness. The two isomers of valeric acid, which occur in high concentrations in the root (Kipping & Kipping, 1959) are the source of their attractiveness to cats. The odour of valeric acid and to a lesser extent iso-butyric acid (but not propionic, butyric, caproic, heptylic or caprylic acid), induce marked changes in behaviour in both male and female cats (Endröczy, Bata & Lissák, 1956). The formerly quiet male develops a lively orientation reaction. He searches about and becomes restless, although nothing characteristic of sexual behaviour is observable. On the other hand, the sexually mature female cat responds to the olfactory stimulus with remarkable sexual behaviour patterns. She becomes restless and licks herself. Stroking the head or

neck by itself produces no change, but mechanical stimulation of the coccygeal area or vulval region leads to characteristic changes. The animal "exhibits sham-rage, performs backward snatches with her head, snarls, assumes the typical lordotic posture and demonstrates the series of motions characteristic of copulation" (Endröczi et al. 1956). Without the olfactory stimulus, stimulation of these regions does not elicit this response. Ovariectomy abolishes the behavioural changes following valeric acid odour, but these changes can be restored by the administration of oestrogen. In the intact animal oestrogen exaggerates the valeric acid-induced behavioural changes whereas progesterone is without effect (Endröczi et al. 1956). The odour of valeric acid was later shown (Lissák, 1962) to evoke electrical activity in the rostral hypothalamus similar to that observed in untreated oestrous cats.

Lissák (1962) further showed that the application of vaginal contents from oestrous cats, onto the nose of an anoestrous cat produced the same behavioural changes and responses to vaginal stimulation as did the odour of valeric acid. Swabs of vaginal secretions from oestrous cats contain detectable amount of valeric acid as measured by gas chromatography (K.P. Bland, unpublished), which suggests a fairly high concentration in the vaginal secretions. These data suggest the existence of a female/female pheromone in the cat such that valeric acid in the vaginal secretions of the oestrous female acts to induce or facilitate oestrus in other females. Inspection of the breeding records of a laboratory cat colony, show that queens in the same harem do in fact come into heat at approximately the same time (D. Hay & T.Graham-Marr, unpublished observations).

CATNIP

It has long been known by cat-owners, as well as big-game hunters (Hart, 1974b), that cats are fascinated by the smell of bruised leaves of Catnip or Catmint (Nepeta cataria, Linnaeus). The smell of the plant produces a characteristic behavioural response (Todd, 1962, 1963b), which includes : sniffing; licking and chewing with head shaking; chin, cheek and body rubbing, and repeated head-over rolling. As early as 1941, McElvain, Bright & Johnson identified the chemical constituents of Oil of Catnip and the following year the same laboratory (McElvain, Walters & Bright, 1942) showed by tests on lions (!) that it was the lactone, NEPETALACTONE, in the oil of catnip that induced the characteristic behaviour. With the identification of the correct chemical structure of nepetalactone (Meinwald, 1954a & b) it was found to have two isomeric forms (Bates, Eisenbraun & McElvain, 1958). The trans-cis-isomer was found to be the one active on cats (Bates & Sigel, 1963). The metabolism of the other isomer (cis-trans-nepetalactone) in the domestic cat has been studied by Waller, Price & Mitchell (1969). Nepetalactone is accumulated in the glands of the leaves of catnip (Regnier, Waller, Eisenbraun & Auda, 1968) and is also present in

other species of Nepeta but in lesser concentrations (Regnier, Waller & Eisenbraun, 1967). However, even in N. cataria its concentration varies between plants from different localities (Regnier, Eisenbraun & Waller, 1967) which may explain why Sakan and co-workers (Sakan, Isoe, Hyeon, Katsumura, Maeda, Wolinsky, Dickerson, Slabaugh & Nelson, 1965) could only find two dihydronepetalactones in extracts of N. cataria cultivated in Japan but were able to extract nepetalactone itself from 3 different samples of commercially prepared oil of catnip (from Canada). A substance closely related to nepetalactone, namely matatabilactone (a mixture of the two isomers of IRIDOMYRMECIN) occurs in the leaves of the shrub Actinidia polygama Miq.; this substance also is attractive to cats (Sakan, Fujino, Murai, Suzui & Butsugan, 1959; Sakan, Fujino & Murai, 1960; Sakan et al. 1965).

By using only the oil of catnip, instead of the whole plant Palen and Goddard (1966) identified the behavioural combination of body rolling and face rubbing as the characteristic reaction to the odour. This behaviour, especially the head-over-rolling is otherwise unique to the behaviour of oestrous females. However, the catnip-response is independent of the sex of the cat or even the presence of the gonads (Todd, 1962, 1963b; Palen & Goddard, 1966), which casts serious doubt on the suggestion that nepetalactone is mimicking a pheromone releasing oestrous behaviour (Todd, 1963b; Hart, 1974b). Besides the domestic cat, the snow leopard, jaguar, leopard, lion, bobcat, lynx, ocelot, puma and several of the smaller cats respond 'sexually' to catnip (Todd, 1963b, 1973). In contrast the adult tiger does not respond while the immature tiger responds by violent alarm and retreating (Todd, 1973) - the kitten of the domestic cat often responds similarly (Todd, 1962). Lion cubs do not respond at all (McElvain et al. 1942).

Todd (1962) found that only a proportion of cats reacted to catnip and by controlled breeding experiments showed that the predisposition to respond was inherited as an autosomal dominant. More recently Hatch (1972) has suggested that nepetalactone is an hallucinogenic agent which induces "pleasurable behaviour" in cats, rather than sexual behaviour as such. This suggestion is supported by the findings in man, that smoking the dried leaves or extract of catnip produces symptoms similar to those produced by the hallucinogenic drugs, marijuana and lysergic acid diethylamide (Jackson & Reed, 1969). By using a wide range of drugs to block the effect of catnip on the central nervous system, Hatch (1972) showed that a number of neural pathways using different transmitters were involved in the feline response to catnip. It would thus appear that nepetalactone can be deleted from the list of feline sexual pheromones or pheromone-mimics and be classed as a feline hallucinogenic agent.

In conclusion there appears to be evidence for at least two sexual pheromones in the cat, namely :

i) 'Tom-cat odour' produced by the male for territorial demarcation but having some oestrous facilitating effect on the female.

ii) Valeric acid or a mixture of fatty acids produced by the oestrous female, and initiating oestrus in other females.

REFERENCES

- Albone, E.S. & Fox, M.W. 1971. Anal gland secretion of the red fox. *Nature*, London 233; 569-570.
- Aronson, L.R. & Cooper, M.L. 1974. Olfactory deprivation and mating behaviour in sexually experienced male cats. *Behavioural Biology* 11; 459-480.
- Bates, R.B., Eisenbraun, E.J. & McElvain, S.M. 1958. The configurations of the Nepetalactones and related compounds. *Journal of American Chemical Society* 80; 3420-3424.
- Bates, R.B. & Sigel, C.W. 1963. Terpenoids. Cis-trans-and trans-cis-Nepetalactones. *Experientia* 19; 564-565.
- Beaver, B.V.G. 1976. Feline Behavioral Problems. *Veterinary Clinics of North America* 6(3); 333-340.
- Boardman, T. 1805. A dictionary of the Veterinary Art. George Kearsley, London.
- Brown, O.P. 1874. The Complete Herbalist. O. Phelps Brown, London.
- Burke, T.J. 1976. Feline reproduction. *Veterinary Clinics of North America* 6(3): 317-331.
- Chamberlin, P.E., Furgason, W.H. & Hall, V.E. 1937. Ketone body excretion in the cat: Sex difference, and influence of diet, fasting, castration and male hormone administration. *Journal of Biological Chemistry* 121; 599-606.
- Cooper, M.L. & Aronson, L.R. 1972. Persistence of high levels of sexual behavior in male cats following ablation of the olfactory bulbs. *American Zoologist* 12(4); 657-658.
- Datta, S.P. & Harris, H. 1951. A convenient apparatus for paper chromatography. Results of a survey of the urinary amino-acid patterns of some animals. *Journal of Physiology* 114; 39-41P.
- Donovan, C.A. 1969. Canine anal glands and chemical signals (pheromones). *Journal of the American veterinary medicine Association* 155; 1995-1996.
- Doty, R.L. & Dunbar, I. 1974a. Attraction of beagles to conspecific urine, vaginal and anal sac secretion odors. *Physiology & Behavior* 12; 825-833.
- Doty, R.L. & Dunbar, I. 1974b. Color, odor, consistency and secretion rate of anal sac secretions from male, female and early-androgenized female beagles. *American Journal of Veterinary Research* 35; 729-731.
- Eaton, R.L. 1970. Group interactions, spacing and territoriality in cheetahs. *Zeitschrift für Tierpsychologie* 27; 481-491.
- Endrőczy, E., Bata, G. & Lissák, K. 1956. Studies on sexual behaviour and its effect on the conditioned alimentary reflex activity. *Acta Physiologica Scientiarum Hungaricae* 9; 153-161.
- Estes, R.D. 1972. The role of the vomeronasal organ in mammalian reproduction. *Mammalia* 36; 315-341.
- Ewer, R.F. 1973. The Carnivores. Weidenfeld & Nicolson, London.
- Fielder, W. 1957. Beobachtungen zum Markierungsverhalten einiger Säugetiere. *Zeitschrift für Säugetierkunde* 22; 57-76.
- Foote, J.J. & Grafflin, A.L. 1938. Quantitative measurements of the fat-laden and fat-free segments of the proximal tubule in the nephron of the cat and dog. *Anatomical Record* 72; 169-179.
- Fox, M.W. 1965. New information on feline behavior. *Modern Veterinary Practice* 46(4); 50-52.
- Fox, M.W. 1971. Feline behavior. *Progress in Feline Practice* 2; 13.
- Fox, M.W. 1975. The behaviour of Cats. In: E.S.E. Hafez (Editor), *The Behaviour of Domestic Animals*. 3rd edition. Baillière Tindall, & Cox. London, pp. 410-436.
- Gairns, F.W. & Morrison, S.D. 1949. Lipid in the nephron of the cat. *Journal of Physiology* 110; 17P.

- Gerber, H.A., Jöchle, W. & Sulman, F.G. 1973. Control of reproduction and of undesirable social and sexual behaviour in dogs and cats. *Journal of Small Animal Practice* 14; 151-158.
- Gowda, C.D.K. 1968. A note on the mating behaviour of tigers, *Panthera t. tigris*, at Mysore Zoo. *International Zoo Yearbook* 8; 63-64.
- Greaves, J.P. & Scott, P.P. 1960. Urinary amino-acid pattern of cats on diets of varying protein content. *Nature*, London 187; 242.
- Greer, M.B. & Calhoun, M.L. 1966. Anal Sacs of the Cat (*Felis domesticus*). *American Journal of Veterinary Research* 27 (118); 773-781.
- Hart, B.L. 1973. Behavioral effects of castration. *Feline Practice* 3(2); 10-12.
- Hart, B.L. 1974a. Feline behavior - Behavioral effects of long-acting progestins. *Feline Practice* 4(4); 8 and 11.
- Hart, B.L. 1974b. Feline behavior - The catnip response. *Feline Practice* 4(6); 8 and 11.
- Hart, B.L. 1975. Spraying behavior. *Feline Practice* 5(4); 11-13.
- Hart, B.L. & Barrett, R.E. 1973. Effects of castration on fighting, roaming, and urine spraying in adult male cats. *Journal of American Veterinary Medicine Association* 163; 290-292.
- Hashimoto, Y., Eguchi, Y. & Arakawa, A. 1963. Histological observation of the anal sac and its glands of a tiger. *Japanese Journal of Veterinary Science* 25; 29-32.
- Hatch, R.C. 1972. Effect of drugs on Catnip (*Nepeta cataria*) - induced pleasure behavior in cats. *American Journal of Veterinary Research* 33; 143-155.
- Helmy, F.M. & Hack, M.H. 1967. Some comparative histochemical studies of the vertebrate kidney. *Comparative Biochemistry & Physiology* 20; 55-63.
- Helmy, F. & Longley, J.B. 1965. Chromatographic analysis of lipid in kidney of the cat and dog. *Anatomical Record* 151; 360.
- Helmy, F.M. & Longley, J.B. 1966. A chromatographic analysis of the lipid of cat and dog kidneys. *Acta Histochemica* 25; 300-311.
- Henschen, F. 1923. In: Joest's *Spezielle Pathologische Anatomie der Haustiere* Vol. 3. p.234. Berlin (Quoted by Hewer et al, 1948).
- Hewer, T.F., Matthews, L.H. & Malkin, T. 1948. Lipuria in Tigers. *Proceedings of the Zoological Society of London* 118; 924-928.
- Jackson, B. & Reed, A. 1969. Catnip and the alteration of consciousness. *Journal of the American Medical Association* 207; 1349-1350.
- Joshua, J.O. 1965. The clinical Aspects of Some diseases of Cats. William Heinemann, London.
- Kipping, F.S. & Kipping, F.B. 1959. *Perkin and Kipping's Organic Chemistry*, Parts I & II. W.&R.Chambers Ltd., Edinburgh.
- Krölling, O. 1927. Entwicklung, Bau und biologische Bedeutung der Analbeuteldrüsen bei der Hauskatze. *Zeitschrift für Anatomie und Entwicklungsgeschichte* 82; 22-69.
- Langley, J.N. & Anderson, H.K. 1895. The innervation of the pelvic and adjoining viscera. Part III. The external generative organs. *Journal of Physiology* 19; 85-121.
- Lissák, K. 1962. Olfactory-induced sexual behaviour in female cats. *Proceedings of the International Union of Physiological Sciences, Leiden (Sept.1962)*. Vol.1(2); 653-656.
- Lobban, M.C. 1951. Variations in the lipid in the kidney of the cat correlated with sexual activity. *Journal of Physiology* 112; 8P.
- Lobban, M.C. 1955. Some observations on the intracellular lipid in the kidney of the cat. *Journal of Anatomy*, London. 89; 92-99.
- McCunn, J. 1953. *Hobday's Surgical Diseases of the Dog and Cat*. Baillière, Tindall & Cox, London.
- McDougal, C. 1977. *The Face of the Tiger*. Rivington Books & André Deutsch, London.
- McElvain, S.M., Bright, R.D. & Johnson, P.R. 1941. The constituents of the volatile Oil of Catnip. I. Nepetalic Acid, Nepetalactone and related compounds. *Journal of the American Chemical Society* 63; 1558-1563.
- McElvain, S.M., Walters, P.M. & Bright, R.B. 1942. The constituents of the volatile Oil of Catnip. II. The neutral components. Nepetalic anhydride. *Journal of the American Chemical Society* 64; 1828-1831.

- Martin, W.D., Fletcher, T.F. & Bradley, W.E. 1974a. Perineal musculature in the cat. *Anatomical Record* 180(1); 3-14.
- Martin, W.D., Fletcher, T.F. & Bradley, W.E. 1974b. Innervation of feline perineal musculature. *Anatomical Record* 180(1); 15-30.
- Meinwald, J. 1954a. The degradation of Nepetalactone. *Journal of the American Chemical Society* 76; 4571-4573.
- Meinwald, J. 1954b. The structure of Nepetalactone. *Chemistry and Industry*, April 24, 488.
- Michael, R.P. 1973. The effects of hormones on sexual behavior in the female cat and rhesus monkey. In: *Handbook of Physiology, Section 7, Volume 2, Part I. American Physiological Society*, pp. 187-221.
- Michael, R.P. & Keverne, E.B. 1968. Pheromones in the communication of sexual status in primates. *Nature, London* 218; 746-749.
- Millot, J. 1927. Sur une fonction d'élimination des graisses par le rein chez les mammifères carnassiers. *Comptes Rendus des Séances de la Société de Biologie* 97; 1474-1476.
- Modell, W. 1933. Observations on the lipoids in the renal tubule of the cat. *Anatomical Record* 57; 13-27.
- Modell, W. & Travell, J. 1934. The role of the lipid in the renal tubule of the cat in uranium nephritis. *Anatomical Record* 59; 253-263.
- Mottram, V.H. 1915-1916. Fatty infiltration of the cat's kidney. *Journal of Physiology* 50; 380-390.
- Mottram, V.H. 1916. Fat infiltration of the cat's kidney. *Journal of Biological Chemistry* 24; xi-xii.
- Nakamura, S. 1935. Beobachtungen über die Fette in den Harnkanälchen von Katze und Hund. *Folia anatomica japonica*, 13; 45-54.
- Palen, G.F. & Goddard, G.V. 1966. Catnip and oestrous behaviour in the cat. *Animal Behaviour* 14; 372-377.
- Regnier, F.E., Eisenbraun, E.J. & Waller, G.R. 1967. Nepetalactone and Epinepetalactone from *Nepeta cataria* L. *Phytochemistry* 6; 1271-1280.
- Regnier, F.E., Waller, G.R. & Eisenbraun, E.J. 1967. Studies on the composition of the essential oils of three *Nepeta* species. *Phytochemistry* 6; 1281-1289.
- Regnier, F.E., Waller, G.R., Eisenbraun, E.J. & Auda, H. 1968. The biosynthesis of Methylcyclopentane monoterpenoids - II. Nepetalactone. *Phytochemistry* 7; 221-230.
- Rosenblatt, J.S. & Schneirla, T.C. 1962. The Behaviour of Cats. In: E.S.E.Hafez (Editor), *The Behaviour of Domestic Animals*. 1st Edition. Baillière, Tindall & Cox, London. pp. 453-488.
- Sakan, T., Fujino, A. & Murai, F. 1960. (1. Extraction of Matatabilactone and Actinidin. 2. Chemical structure of Matatabilactone). *Nippon Kagaku Zasshi* 81; 1320-1326 (in Japanese).
- Sakan, T., Fujino, A., Murai, F., Suzui, A. & Butsugan, Y. 1959. The structure of Matatabilactone. *Bulletin of the Chemical Society of Japan*. 32(10); 1154-1155.
- Sakan, T., Isoe, S., Hyeon, S.B., Katsumura, R., Maeda, T., Wolinsky, J., Dickerson, D., Slabrough, M. & Nelson, D. 1965. The exact nature of Matatabilactone and the Terpenes of *Nepeta cataria*. *Tetrahedron Letters* No. 46; 4097-4102.
- Schaffer, J. 1940. *Die Hautdrüsenorgane der Säugetiere* Urban & Schwarzenberg, Berlin.
- Schaller, G.B. 1969. *The Deer and the Tiger*. University of Chicago Press, Chicago.
- Schaller, G.B. 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press, Chicago.
- Schenkel, R. 1966. Play, exploration and territoriality in the wild lion. *Symposium of the Zoological Society of London* 18; 11-22.
- Seidenberg, L., Kornick, H.P. & others 1975. Panel Report: Spraying by castrated tomcats. *Modern Veterinary Practice* 56(10); 729-731.
- Short, R.V. 1972. Role of hormones in sex cycles. In: C.R. Austin and R.V. Short (Editors), *Reproduction in Mammals. Book 3 - Hormones in Reproduction*. Cambridge University Press, Cambridge.

- Smith, C. 1920. A study of the lipoid content of the kidney tubule. *American Journal of Anatomy* 27; 69-97.
- Smith, C. & Freeman, B.L. 1954. Distribution of lipids, lipase and alkaline phosphatase in renal tubules of the cat. *Proceedings of the Society for Experimental Biology and Medicine* 86; 775-778.
- Tallan, H.H., Moore, S. & Stein, W.H. 1954. Studies on the free amino acids and related compounds in the tissues of the cat. *Journal of biological chemistry* 211; 927-939.
- Todd, N.B. 1962. Inheritance of the Catnip response in domestic cats. *Journal of Heredity* 53; 54-56.
- Todd, N.B. 1963a. Behavior and genetics of the domestic cat. *The Cornell Veterinarian* 53(1); 99-107.
- Todd, N.B. 1963b. The Catnip Response. Doctoral dissertation, Harvard Biological Laboratories. Quoted in Ewer (1973).
- Todd, N.B. 1973. Unpublished work quoted in Ewer (1973).
- Treutlein, ?, Lehmann, K.B. & Ruppel, ?. 1914. Untersuchungen über den histologischen Bau und den Fettgehalt der Niere der Katze. *Frankfurter Zeitschrift für Pathologie* 15; 163-180.
- Verbene, G. 1970. Beobachtungen und Versuche über das Flehmen Katzenartiger Raubtiere. *Zeitschrift für Tierpsychologie* 27; 807-827.
- Vulpian, M.A. 1861. Sur la présence de la graisse, à l'état normal, dans les reins et dans l'urine des chiens et des chats adultes. *Comptes Rendus des Séances de la Société de Biologie*. 13; 267-269.
- Waller, G.R., Price, G.H. & Mitchell, E.D. 1969. Feline attractant, cis, trans-Nepetalactone: Metabolism in the domestic cat. *Science* 164; 1281-1282.
- Westall, R.G. 1953. The amino acids and other ampholytes of Urine. 2. The isolation of a new sulphur-containing amino acid from cat urine. *Biochemical Journal* 55; 244-248.
- Whitehead, J.E. 1971. Tomcat spraying. *Progress in Feline Practice* 2; 13-14.
- Worden, A.N. 1959. Abnormal behaviour in the dog and cat. *Veterinary Record*. 71; 966-978.