5 The signalling repertoire of the domestic cat and its undomesticated relatives

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Introduction

Previous accounts of communication between domestic cats (e.g. Bradshaw, 1992) have been largely based on a traditional ethological approach. The signals and the context in which they occur have been described, and related to the kind of environment signaller and receiver can expect to find themselves in, and to the sensory capabilities of the receiver. For example, this approach explains the use of scent signals by domestic cats as products of both their acute sense of smell, which may have evolved primarily in relation to detection of food, and also their origin as territorial animals which needed to communciate with neighbours that they might rarely encounter face-to-face. However, modern biological signalling theory is equally concerned with what information is being transferred and how it is transmitted (Grafen & Johnstone, 1993). More specifically, it examines how signals can become evolutionarily stable, given that the interests of emitter and recipient are often not identical.

Communication is said to occur when one animal responds to the signals sent out by another. This is a more general definition than normally applies to communication between people, when it is usually assumed that information is being exchanged, and is reasonably accurate. Unfortunately there has been a tendency to carry this 'conventional' definition over to communication between animals, implying that animals that are signalling to one another agree about the message being transmitted (Zahavi, 1993). In many instances there is no reason to believe that this is the case; signallers often attempt to manipulate the behaviour of recipients to their own advantage, while recipients attempt to 'mind-read' these deceptions (Krebs & Dawkins, 1984). This kind of theoretical framework has hardly ever been applied to signalling in the domestic cat; in this chapter we have attempted to speculate as to the evolutionary origins of some signals, such as the odour of tom-cat urine, purring, and agonistic visual signals.

The influence of domestication on signalling adds a further dimension to the explanation of why signals take the form they do. In the case of the cat, the ancestral species *Felis silvestris libyca* is thought to be exclusively territorial, and so its signalling repertoire must presumably have changed as it evolved to live at high densities and to become facultatively sociable. When individual animals live close together, and benefit by cooperation, they need the ability to resolve conflicts without resorting to physical violence, particularly when both protagonists are as well-armed as a cat. It is not yet certain when this ability arose, since the social biology of *F. libyca* has been little studied, but in the second part of this chapter we have attempted to examine the extent to which domestication has influenced the signalling repertoire of the domestic cat, by comparing it with that of other, undomesticated, Felidae. In the first part we describe the signals performed by the domestic cat itself, and their presumed functions.

Communication between domestic cats

Olfactory communication

The ancestral species of the domestic cat, *F. s. libyca*, is probably exclusively territorial (Smithers, 1983; Happold, 1987; Macdonald, 1996), as are most of the smaller species in the Felidae. Since widely-spaced animals rarely encounter one another face-to-face, they tend to communicate by scent-marks, which permit a delay of several hours or days between the deposition of the signal and its reception. For well-armed carnivores, there is also the advantage that potentially dangerous encounters with rivals can be avoided by the use of olfactory signals, both those deposited on the substratum and those that are carried directly from the body surface by air currents. The potential disadvantage of relying on scent signals is lack of control, both of the direction the message is carried in, which is at the mercy of the wind, and of who receives it, since a scent-mark cannot be switched off at will; both lead to potential exploitation of the information that the scent contains. Despite these problems, members of the Carnivora rely extensively upon scent for communication (Gorman & Trowbridge, 1989).

Many domestic cats live at a density several orders of magnitude higher than their wild counterparts (see Chapters 6 and 7), and it is therefore possible that their scent communication has been modified during the course of domestication. Cats that live in groups can potentially not only exchange information through scents, but also exchange the scents themselves to produce colony- or group-specific odours (Gorman & Trowbridge, 1989). Comparisons with other species therefore suggest that the domestic cat should have a complex and versatile repertoire of

scent signals, so it is perhaps surprising that comparatively little research has been conducted in this area. While several sources of odours have been documented, their functions in communication are generally still speculative.

Urine

Cats can adopt two distinctly different postures for urination, indicating that at least one has some use in signalling. Kittens, juveniles and adult females usually squat to urinate and then usually cover the urine with soil or litter. Although this can be interpreted as an attempt to hide the urine, and so presumably the information that its odour contains, such deposits are sniffed by other cats if encountered. Moreover, the duration of sniffing tends to increase with the unfamiliarity of the depositor, suggesting that the sniffer is responding to and gathering information from the odour (Passanisi & Macdonald, 1990). This may only be a common occurrence where cats are living at high densities; the attempted concealment may be effective in widely-spaced territories.

Deliberate scent-marking with urine is performed by spraying, in which the cat backs up to a vertical surface, and urinates backwards, usually while quivering its tail. While mature males are the most frequent sprayers, adult females do also spray. In closed or high-density colonies there may be some suppression of spraying in females and younger males, resulting in most spray-marks being produced by a small number of 'dominant' males (Natoli, 1985; Feldman, 1994a). Spraying by tom-cats is enhanced by the proximity of oestrous females, resulting in an annual peak (in the UK) in February/March (Feldman, 1994a).

The odour of sprayed urine is pungent, prompting speculation that it carries other secretions, possibly from the preputial or anal glands (Wolski, 1982). The anal gland secretion, which is voided by very frightened cats, certainly has a distinctive odour, but this is not, to the human nose, similar to that of sprayed urine. The odour of sprayed urine increases after deposition (Joulain & Laurent, 1989), and is probably largely due to the microbial and oxidative degradation of the two unusual amino-acids which it contains, felinine (L-2-amino-7-hydroxy-5,5-dimethyl-4-thiaheptanoic acid, I) and isovalthene (2-amino-5-carboxy-6-methyl-4-thiaheptanoic acid) (Westall, 1953; Oomori & Mizuhara, 1962). The main degradation products, 3-mercapto-3-methyl-1-butanol (II) and 3-methylthio-1-butanol (III), and other disulphides and trisulphides, have strong 'tom-cat' odours (Joulain & Laurent, 1989; Hendricks *et al.*, 1995a). Entire males can excrete large amounts of felinine, up to 95 mg/day, whereas females produce less, up to about 20 mg/day, which correlates with the lesser pungency of female sprayed urine. Hendricks *et al.* (1995b) have suggested that this excretion may have a significant effect on the sulphur-containing amino-acid requirements of an entire male, since felinine is biosynthesised from cysteine and possibly taurine. It is therefore possible that the amount of felinine in the urine, and hence the strength of its odour, is an accurate reflection on the success of the male in obtaining high-quality food, and is therefore an 'honest' signal (Zahavi & Zahavi, 1997) advertising his fitness as a mate (to females) and competitor (to other males).

The territorial function of urine-spraying, if any, is unclear. Spray-marks are rarely observed to act as a deterrent in their own right, but this is the case for most territorial scent-marks (Gosling, 1982), even those which mark the edges of territories, which those of tom-cats do not (Feldman, 1994a). It has also been suggested that since the odour of scent-marks changes with age, they could be used to assist cats to space themselves out while hunting, so that they could avoid areas which had been disturbed recently (Leyhausen, 1979). However, this is unlikely to be a stable strategy; cats that did not spray-urinate could put themselves at an advantage because other cats would waste time and effort hunting in places where prey was still wary due to the recent proximity of a predator.

All cats, but particularly adult males, investigate spray-marks intently (Natoli, 1985; Matter, 1987; Passanisi & Macdonald, 1990), particularly if they are produced by oestrous females (Verberne & de Boer, 1976) which suggests that they do contain relevant information. Initial inspection is usually by sniffing, often followed by *flehmen*, in which the upper lip is raised and the mouth held partially open; this may persist for half a minute or more. During flehmen the cat may make physical contact with the source of the odour, and moves its tongue to and fro behind its incisors, where the openings of the ducts that lead to the vomeronasal organs (VNO) lie. Both airborne and fluid-borne molecules of the odorant are thereby carried into the VNO (Hart & Leedy, 1987), which is an accessory olfactory organ of unknown function (in the cat). Since flehmen is only performed in response

to odours from other cats, it presumably gathers (and possibly stores) social information.

Faeces

Many species within the Carnivora use faeces, often with glandular secretions added, to convey information (Gorman & Trowbridge, 1989), but the evidence that domestic cats do this is only circumstantial. Near to the core of the home range, faeces are usually buried (Feldman 1994a), but they may be left exposed elsewhere (Macdonald *et al.*, 1987). Cats usually sniff the places where they have just buried faeces, but tend not to do so after leaving them exposed (Macdonald *et al.*, 1987). This suggests that one of the functions of burying faeces is to minimise the likelihood that the olfactory information they contain will be detected by another cat, although hygiene may provide a more parsimonious explanation. Attempts to demonstrate that unburied faeces serve as territorial markers have produced equivocal results (Dards, 1979; Macdonald *et al.*, 1987; Feldman, 1994a).

Scratching

Although it undoubtedly has a role to play in the conditioning of the claws of the front feet, scratching must inevitably result in the deposition of scent from the glands on the paws (interdigital glands) (Ewer, 1973). The same scratching site is often used over and over again, resulting in a clear visual marker which presumably draws attention to the olfactory information, although there appear to be no published studies which report the extent to which scratched sites are sniffed. The scratching sites are distributed along regularly-used routes, rather than at the periphery of the territory or home-range (Feldman, 1994a).

Skin glands

Domestic cats have several skin glands (Prescott, cited in Fox, 1974); in addition to the interdigital glands mentioned above, these include; the submandibular gland beneath the chin, the perioral glands at the corners of the mouth, temporal glands on each side of the forehead, a gland at the base of the tail (which can over-secrete in entire males, giving rise to the condition 'stud-tail'), and caudal glands, which are diffusely distributed along the tail (Wolski, 1982). The pinnae (external ears) also produce a waxy secretion.

It is unclear whether each of these glands produces a unique secretion, each with a well-defined function, or whether there is considerable overlap. The secretions of the glands on the head are rubbed on to prominent objects by a behaviour pattern known as bunting (Houpt & Wolski, 1982). The precise form of this appears to depend upon the height of the object being rubbed, such that high objects are primarily marked with forehead and ears, objects at head height with a wipe of the head from the corner of the mouth to the ear, and lower objects with the underside of the chin and then the side of the throat (Verberne & de Boer, 1976). This plasticity suggests that similar odours are deposited from all parts of the head, either because there is redundancy between the glandular secretions themselves, or because they become thoroughly mixed on the coat through grooming.

Entire adult males tend to rub-mark more frequently than do anoestrous females or juveniles (Feldman, 1994a) and occasionally spray urine on top of their own rub-marks (Dards, 1979; Panaman, 1981) or vice versa (Macdonald *et al.*, 1987). Other rub-marks, although performed on visually prominent objects, such as projecting twigs or corners of man-made structures, are not associated with any other visual or obvious olfactory cue and are thus not obvious to the human observer. Cats, on the other hand, appear to be able to locate them easily, suggesting that they are quite pungent to the feline nose, and frequently over-mark them with their own cephalic secretions. The rub-marks of entire females contain information about the oestrus cycle, as indicated by the degree of interest shown by males (Verberne & de Boer, 1976), but apart from this there is little published information on the function of this behaviour. Some cats also rub-mark repeatedly in the vicinity of humans, but this may possibly be a displaced version of cat–human rubbing (Moore & Stuttard, 1979).

Cat–cat rubbing is a visual and tactile display which must also result in the exchange of odours between the pelages of the participating cats, although it is unclear whether this has any relevance, for example in the establishment of 'group odours' shared by cats that are friendly towards one another. When cats sniff each other, they tend to concentrate on the head region, rather than the flanks and tail where shared odours would presumably accumulate, suggesting that even if group odours do exist, individual odours contain more valuable information.

Auditory communication

Cats' vocalisations are largely restricted to four types of interactions; agonistic, sexual, mother–young, and cat–human. Most of the aggressive and defensive sounds (Table 5.1) are strained-intensity calls (Moelk, 1944), since under these circumstances the cat is likely to be tensing its whole body in preparation for a fight. Tension in the throat is presumably the reason why cats drool during fights, or have to break off from vocalising to swallow repeatedly. The low pitch of the growl and the long duration of the yowl are presumably designed to convey the size and strength of the cat that is emitting them, and the abruptness and volume of the pain shriek may be designed to shock or startle the attacker into loosening its grip. Both the female and male sexual calls (Table 5.1) are also of high intensity, presumably advertising fitness to potential sexual partners and rivals of the same sex (see Chapter 7).

The calls produced by kittens less than three weeks old are restricted to the defensive spit, purring, and a distress call which has aural characteristics similar to the adult miaow (see Figure 5.1). The latter is given when the kitten becomes isolated, or cold, or trapped, for example, if its mother accidentally lies on top of it (Haskins, 1979). The call induced by cold is significantly higher pitched than the other two, although this distinction disappears as the kitten becomes capable of thermoregulation at about four weeks of age. Restraint induces a call which is similar in pitch to that caused by isolation, but is significantly longer in duration, and the isolation call is generally the loudest (Haskins, 1979). It is therefore likely that mother cats can distinguish between these calls, and respond accordingly (Haskins, 1977).

Purring is a ubiquitous vocalisation among cats, but its function is not entirely understood and, until recently, its method of production was not entirely clear. It is produced during both inhalation and exhalation, except for a brief pause at the transition between the phases of the respiration cycle, and therefore sounds as if it is a continuous vocalisation. The sound is generated by a sudden build-up and release of pressure as the glottis is closed and then opened, resulting in a sudden separation of the vocal folds, which generate the sound (Remmers & Gautier, 1972). The laryngeal muscles which move the glottis are driven by a free-running neural oscillator, generating a cycle of contraction and release every 30–40 milliseconds (Frazer-Sissom, Rice & Peters, 1991).

Table 5.1. *Characteristics of the vocal signals used by adult domestic cats, compiled from Moelk (1944), Brown et al. (1978) and Kiley-Worthington (1984), and the circumstances under which each is most commonly used.*

Name	Typical duration (s)	Fundamental pitch (Hz)	Pitch change	Circumstances
Sounds produced with the mouth closed				
Purr	2+	25–30	–	Contact
Trill/chirrup (F)[a]	0.4–0.7	250–800	Rising	Greeting, kitten contact
Sounds produced while the mouth is open and gradually closed				
Miaow (B)	0.5–1.5	700–800	–	Greeting
Female call	0.5–1.5	?	Variable	Sexual
Mowl (male call)	?	?	Variable	Sexual
Howl (D)	0.8–1.5	700	–	Aggressive
Sounds produced while the mouth is held open in one position				
Growl	0.5–4	100–225	–	Aggressive
Yowl (D)	3–10	200–600	Rising	Aggressive
Snarl	0.5–0.8	225–250	–	Aggressive
Hiss (E)	0.6–1.0	Atonal	–	Defensive
Spit	0.02	Atonal	–	Defensive
Pain shriek (C)	1–2.5	900	Slight rise	Fear/pain

[a]Refers to Table 1 of Brown *et al.* (1978).

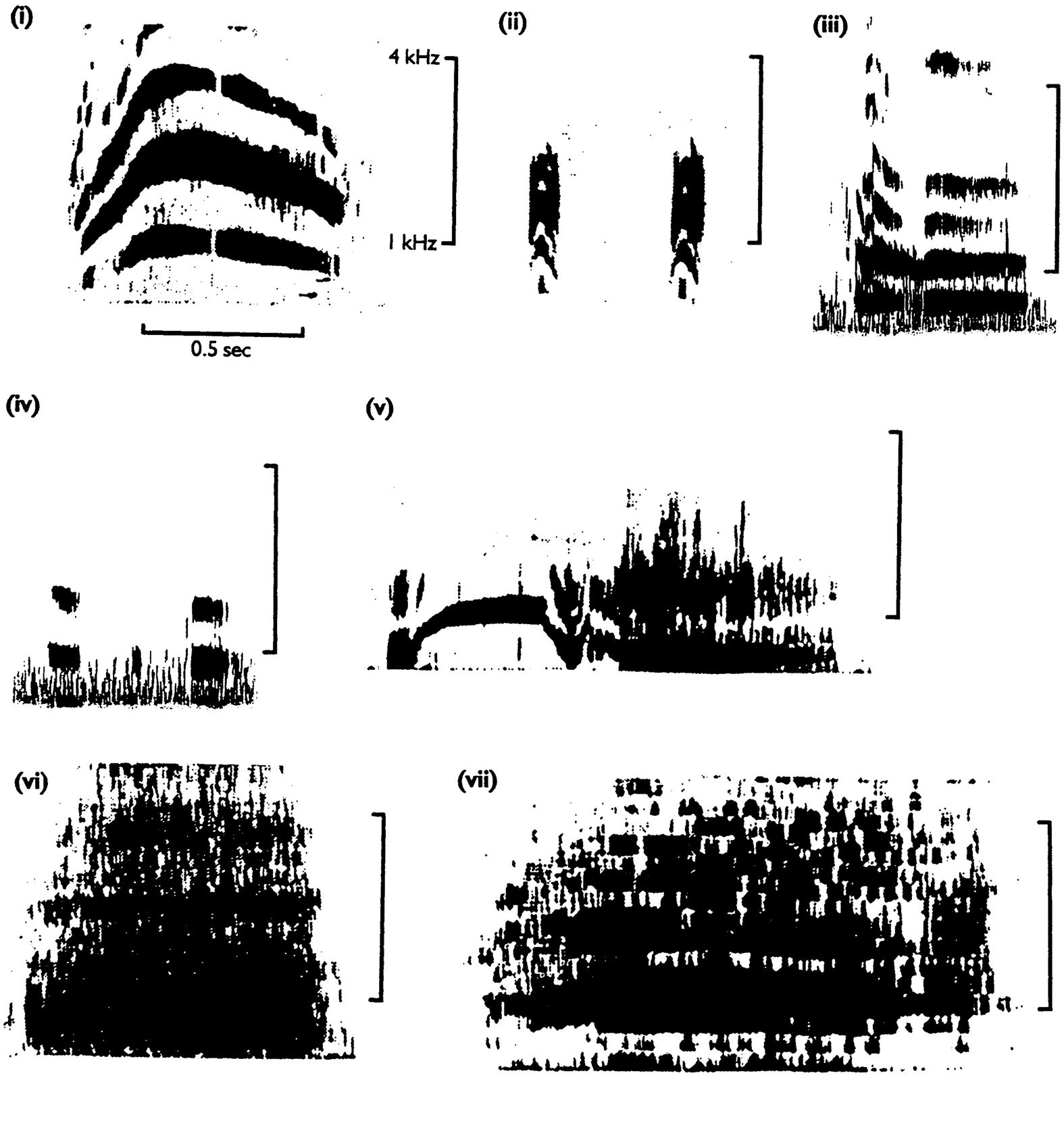


Figure 5.1. Sonagraphs of typical kitten and cat vocalisations. (i) Kitten isolation call. (ii) Maternal chirrup. (iii) Miaow (typical). (iv) Miaow (atypical). (v) Howl. (vi) Hiss. (vii) Pain shriek. (iii) and (iv) provided by Jean-Luc Renck; others from Brown *et al.* (1978).

Although it is traditional to interpret purring as indicating 'pleasure', it is produced in a wide variety of circumstances, most of which involve contact between the cat and a person or another cat. Kittens are able to purr almost from birth, and do so primarily when they are suckling, which may induce the mother to continue to nurse them (Haskins, 1977). Adult cats may purr when in contact with a familiar partner, and during tactile stimulation with inanimate objects, such as when rolling or rubbing (Kiley-Worthington, 1984). All of these circumstances can be conceived of as potentially pleasurable to the cat, but there is one serious exception to this: veterinarians commonly experience cats that purr continuously when they are chronically ill or appear to be in severe pain (Beaver, 1992). Purring may therefore function as a 'manipulative' contact- and care-soliciting signal, possibly derived from its (presumed) function in the neonate.

Apart from purring, the vocalisation that is commonest in cat–human interactions is the miaow. This is very rarely heard during cat–cat interactions (Brown, 1993) and may therefore be a learned response, based upon its effectiveness in getting human attention. It is certainly very easy to train in food-deprived cats; Farley *et al.* (1992) were able to induce a rate of two miaows per minute for a period of two hours or more. There are also considerable variations in frequency, duration and form of the miaow, both within and between individuals (Figure 5.1. iii, iv) (Moelk, 1944) which argue against the miaow having an (intra)species-specific meaning. It is therefore likely that each cat learns by simple association that miaowing induces feeding, access to desired locations, and other resources provided by humans, and that some cats can learn to produce different miaows for different purposes.

Visual communication

Wild-type (striped tabby) domestic cats are cryptically marked, and have no obvious structures that have been specially adapted for signalling. Despite its relatively immobile flat face, compared with the wolf, the cat has quite a varied repertoire of visual signals,

mainly used in regulating aggressive behaviour. There is no evidence to suggest that any of the changes to the pelage introduced post-domestication (e.g. orange, white spotting, long hair) have had any substantial effect upon ability to signal, in contrast to the profound loss of visual signalling structures in some breeds of dog (Goodwin, Bradshaw & Wickens, 1997).

Many of the postures adopted in agonistic encounters can be interpreted as attempts by the cat to alter its apparent size, and thereby influence the outcome of the interaction. An aggressive cat will piloerect and stand at its full height, whereas a cat that wishes to withdraw from a contest will crouch on the ground, flatten its ears (Figure 5.2), and withdraw its head into its shoulders, indicating that it is not ready to launch a biting attack (Figure 5.3). The defensive–aggressive posture (bottom right of Figure 5.3) is presented when the aggressor is about to press home its attack (and also to potential predators such as dogs). This is usually adopted side-on to the opponent, doubtless to maximise its visual impact. Although more extreme, it is similar in form to the 'Side-step' posture used by kittens in play; since this posture tends to disrupt

Figure 5.2. Ear postures associated with aggression and defence. From UK Cat Behaviour Working Group (1995).

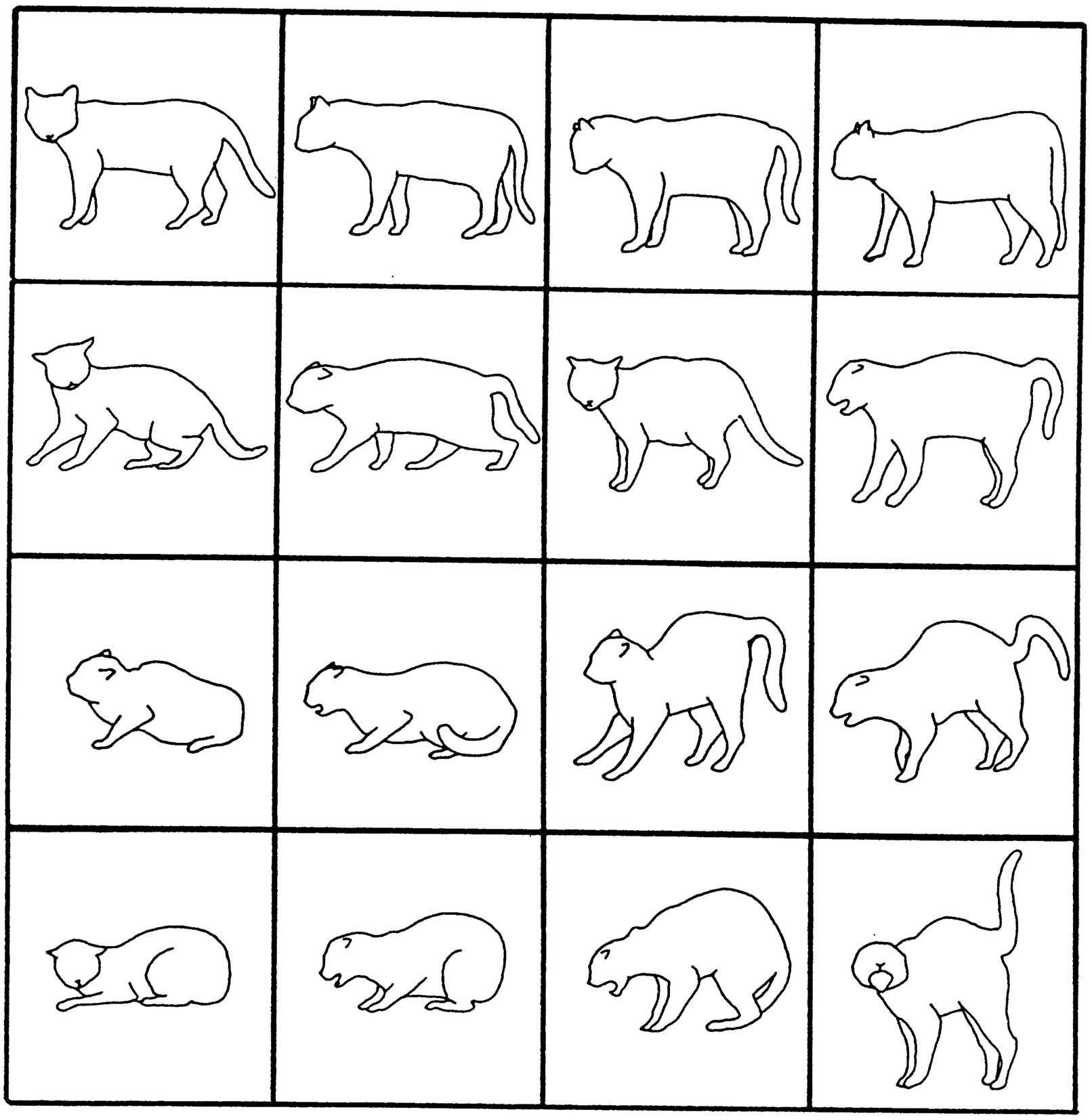


Figure 5.3. Whole-body postures associated with aggression (increasing from left to right) and fear/submission (increasing from top to bottom). Redrawn from Leyhausen (1979).

bouts of social play (West, 1974), it is likely that one is the developmental antecedent of the other.

Presumably all of these postures are interpreted by the cat's opponent, and used in deciding how to proceed in the encounter, but there is little direct evidence as to how each posture influences its outcome. Competitive encounters between animals of the same species tend to involve signals which are both unsubtle, and aimed at manipulating the behaviour of the recipient, which should attempt to combat this by 'mind-reading' (Krebs & Dawkins, 1984). The agonistic displays of cats are certainly easy to see, but the extent to which each posture is a form of 'bluffing', and how effective each is at deceiving its recipient, remain to be investigated.

In the preliminary stages of agonistic encounters, cats tend to avoid looking at one another. In a study of staged 4-minute pairwise encounters between neutered cats from the same colony, D. Goodwin and J. Bradshaw (unpublished data) recorded that each cat looked at the other 1.8 times per minute on average. In encounters that involved agonistic behaviour or signals, the amount of time that the two cats looked at each other simultaneously (mutual gaze) was less than predicted from the total amount of time that each spent looking at the other. In other words, each cat monitored the position of the other, but tended to look away before being looked at: in these circumstances, mutual gaze may be being interpreted as a threat signal. In encounters with no agonistic content, the amount of mutual gaze was not different from that predicted from the amount of time that each looked at the other, and so may not be being used a signal.

Rolling is a component of female sexual (pro-estrus) behaviour, where it is usually accompanied by purring, stretching and rhythmic opening and closing of the claws, and is interspersed with bouts of object-rubbing (Michael, 1961). Male-to-male rolling appears to be a form of submissive or appeasement behaviour, since it is never directed by mature males towards immature males, and is often followed by the mature male ignoring or tolerating the immature male's presence (Feldman, 1994b).

The cat's highly mobile tail, with its independently

movable tip, appears admirably suitable for use as a signalling organ as well as assisting in balance. The tail is tucked away between the hind legs in the submissive/defensive posture (bottom left of Figure 5.3), but this is unlikely to convey much information that is not already provided by the posture itself. Lashing of the tail from side to side is a component of aggressive behaviour (Kiley-Worthington, 1976), but its value as a signal is unknown.

The vertically-held tail (tail-up, TU) is associated with affiliative behaviour (Brown, 1993; Bernstein & Strack, 1996), but its function as a signal has only recently been elucidated. In a colony of neutered feral cats, Cameron-Beaumont (1997) found that TU was particularly associated with rubbing on and sniffing of another colony member (TU occurred in more than 80 per cent of these interactions). Almost all bouts of cat–cat rubbing were preceded by the initiating cat approaching with its tail up, and the probability of the rubbing occurring was further enhanced if the recipient cat also raised its tail (Figure 5.4). She confirmed the role of TU as a signal, and not simply a correlate, of affiliative behaviour, by presenting pet cats with silhouettes identical apart from the position of the 'tail'. The TU silhouette (Figure 5.5) was significantly more likely to induce TU when it was first sighted by the responding cat, and was also approached faster than the silhouette with its tail down, which induced some tail-swishing or tail-tucked postures. The vertical tail therefore signals an intention to interact amicably; presumably it is necessary because of the potentially dire consequences of being approached by a cat whose intentions are unknown.

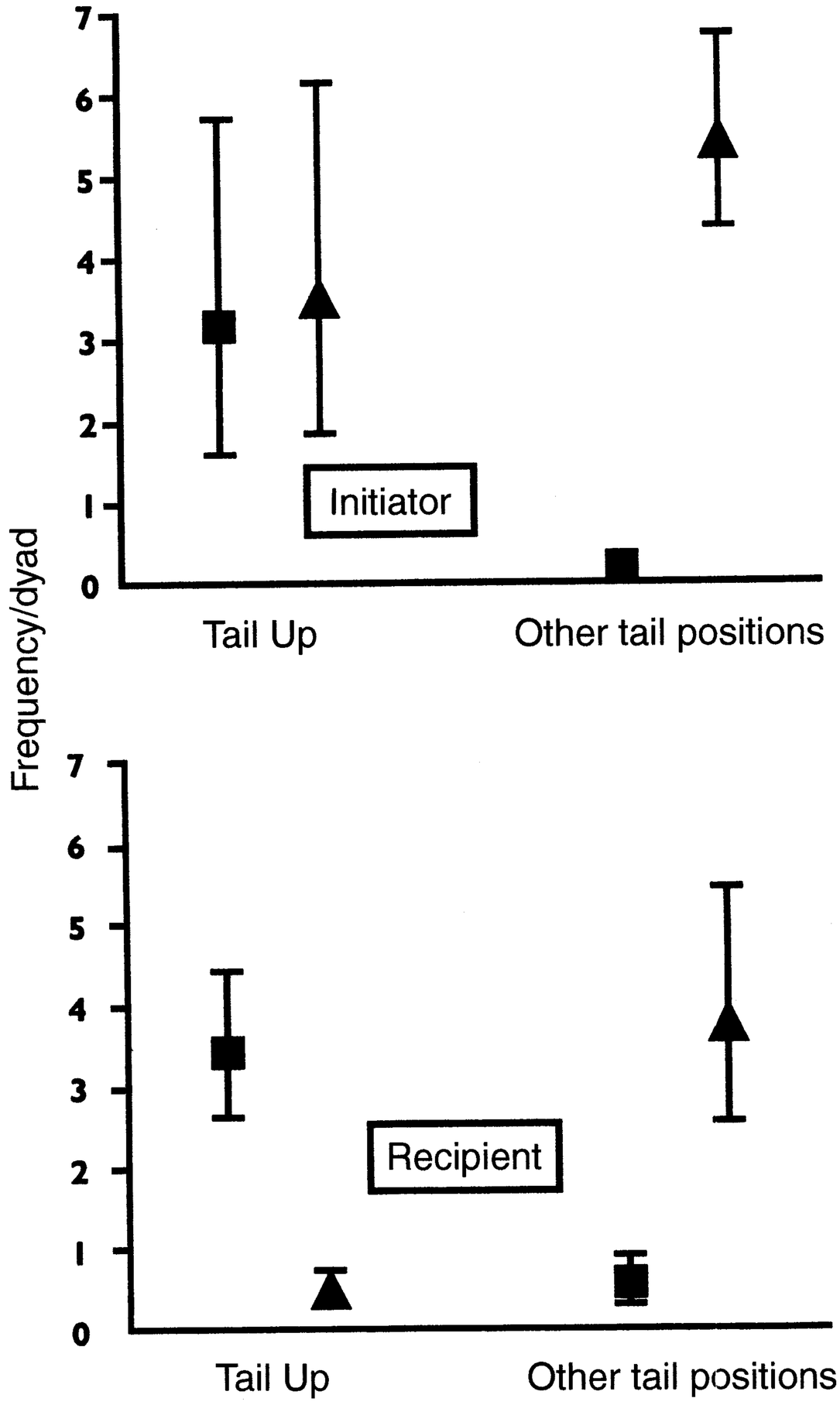


Figure 5.4. Association between the Tail Up posture by the initiator (upper graph) and recipient (lower graph), and rubbing (■) and other types of interaction (▲), compared to all other tail postures (the rare Tail Half-Up posture is omitted). Only Tail Up approaches by the initiator are included in the lower graph. Frequencies are averages per dyad in a free-ranging neutered colony (2 male, 3 female) during 34 hours of observation. From Cameron-Beaumont (1997).

Tactile communication

Although simple physical contact, as when two cats rest together, may have social significance, the two most obvious forms of tactile communication are cat–cat rubbing their heads, flanks or tails on one another (allorubbing), and one cat licking another (allogrooming).

Even though Macdonald *et al.* (1987) proposed that 'cats in net receipt of rubbing would enjoy the benefits of dominance and, within their sex, greater inclusive fitness', little evidence has been forthcoming subsequently to confirm or refute this. In a breeding farm colony, they found that the flow of rubbing was asymmetrical in the majority of dyads, being skewed (a) from adult females to the male, (b) within adult females, (c) from kittens to adult females (Figure 5.6). Asymmetry in the flow of rubbing within dyads was also detected by Brown (1993) among neutered feral cats. She also found that interactions involving sitting together and allogrooming were unlikely to be preceded (or followed) by rubbing, which supports the suggestion of Macdonald *et al.* (1987) that rubbing tends to take place between cats of unequal size or status. Further research is needed to fully elucidate

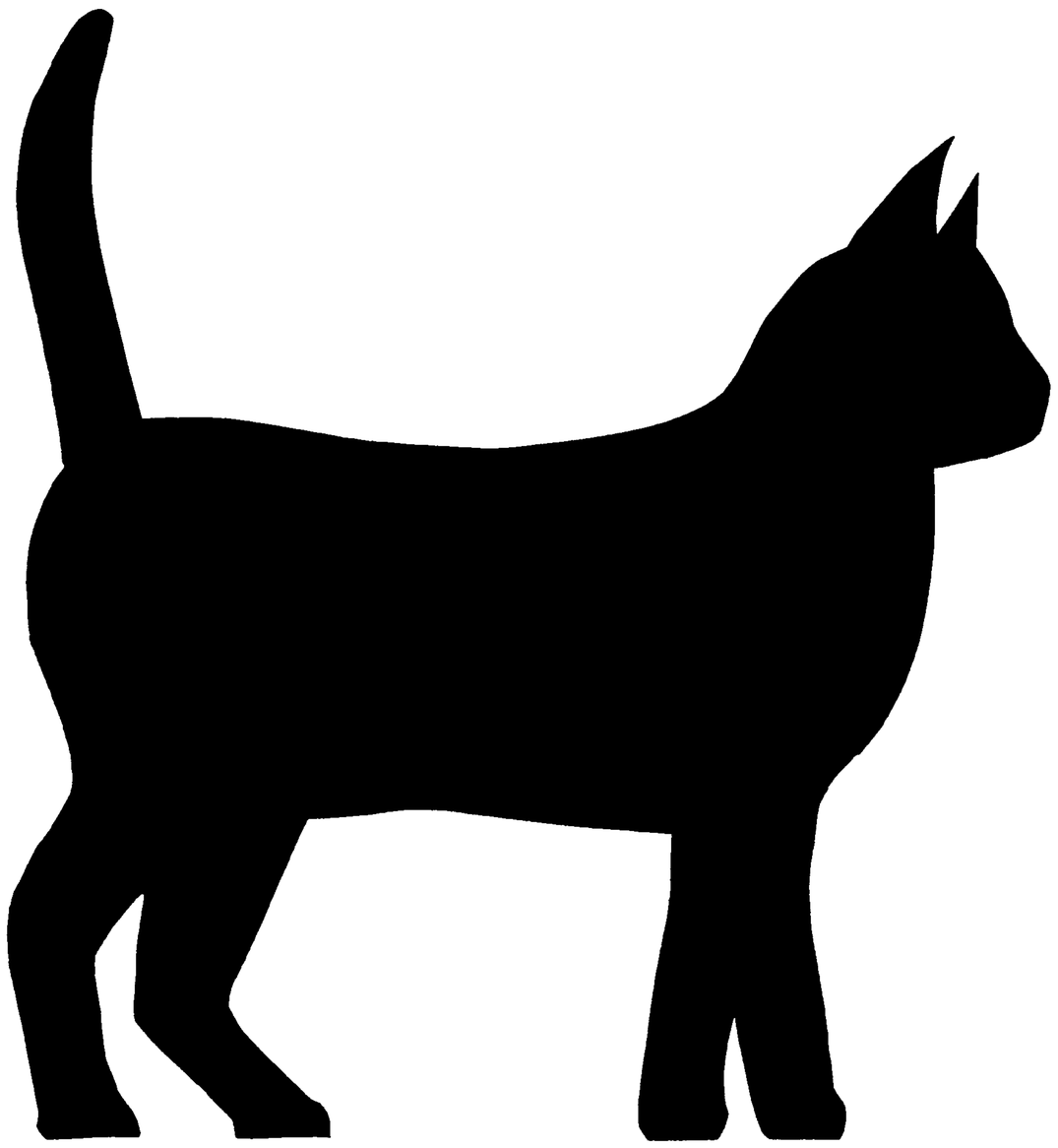


Figure 5.5. Cat-sized silhouette used to investigate the signalling function of the TU posture. The silhouette used for comparison had its tail sloped down towards the ground, with its tip horizontal.

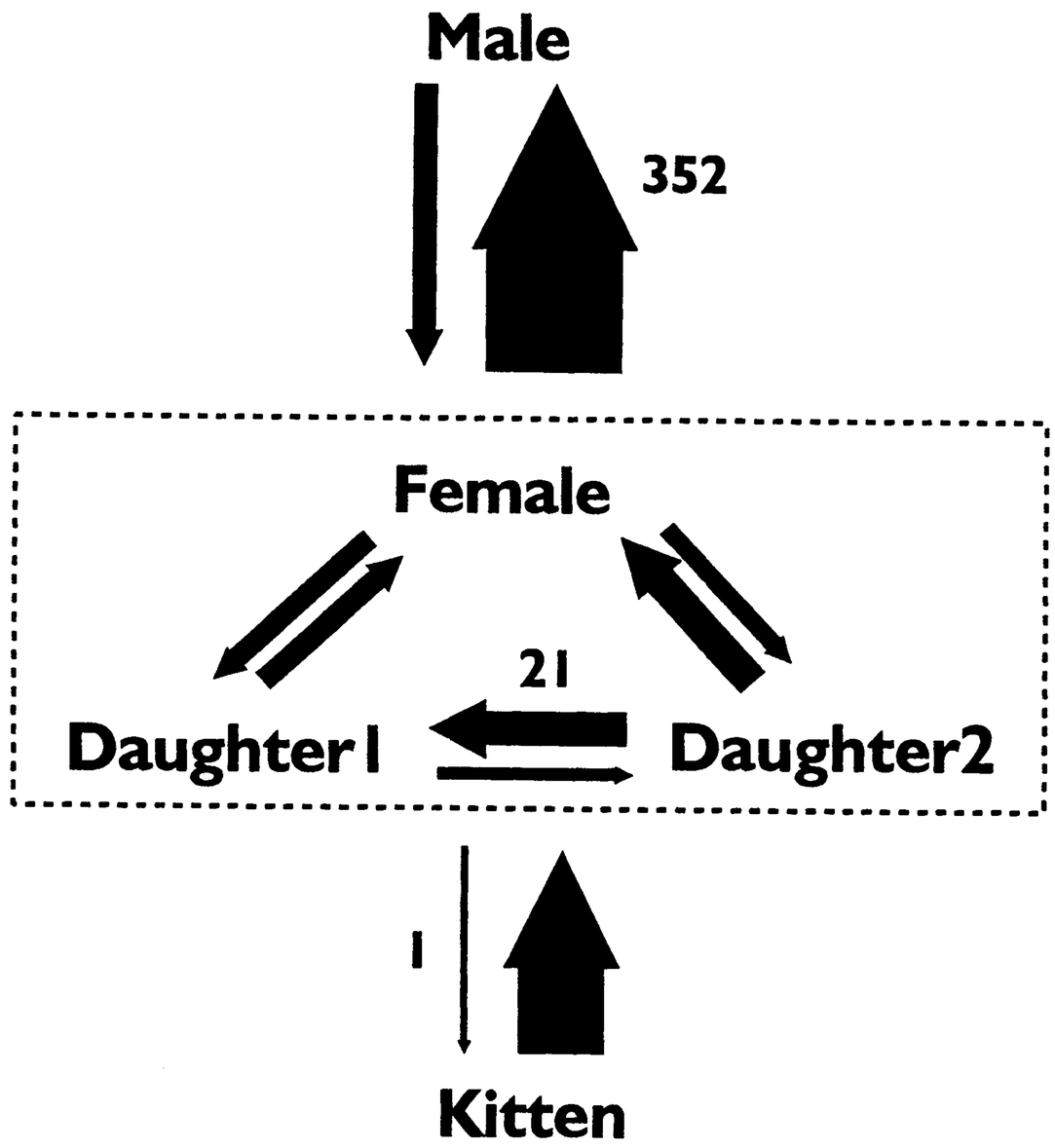


Figure 5.6. Frequencies of cat–cat rubbing in a farm colony of five cats, comprising a female, her two adult daughters, an adult male, and a male kitten. Widths of arrows are proportional to the square root of the number of rubbing interactions performed over an 8-month period (6 months for the kitten) by each age/sex-class towards every other, and within the female sex class. Actual numbers of interactions are indicated for the largest, smallest and one intermediate arrow. All pairs of arrows indicate a significantly assymetric performance of rubbing, except that between the Female and Daughter 1. Data from Macdonald *et al.* (1987).

the social meaning of rubbing, including whether the transfer of scent that must inevitably take place has any significance.

While grooming of one member of a social group by another has significance in many species (Wilson, 1975) it is only recently that Ruud van den Bos (1998) has begun to elucidate its role in the domestic cat. In an indoor colony consisting of 14 neutered males and 11 neutered females, the more aggressive individuals groomed the less aggressive more often than the other way around. In about one-third of the interactions, groomers were also aggressive towards the cats they were grooming, often immediately after the bout of grooming had finished. These results are consistent with the idea that allogrooming in the domestic cat is a form of redirected aggression or dominance behaviour. He found no evidence for any effect of kinship on the choice of partners for allogrooming (relatedness coefficients within the colony varied between 0 and >0.6), which tends to argue against a role in maintaining bonds between kin. However, the possibility remains that allogrooming has other roles in free-ranging breeding colonies.

Functional organisation of signals between domestic cats

Various techniques have been used to combine communicative patterns together into groups with overlapping functions, including subjective methods (Kerby, 1987), differences between pairwise relationships (van den Bos & de Vries, 1996) and probability of performance by an individual cat within a single interaction (Brown, 1993; Cameron-Beaumont, 1997). Direct comparisons between these studies are not straightforward, since different ethograms have been used, and different social compositions observed (Kerby: free-ranging breeding farm cats; van den Bos and de Vries: indoor colonies of breeding females; Brown, Cameron-Beaumont: neutered, mixed-sex indoor and free-ranging colonies). Cameron-Beaumont, reanalysing data collected by Brown from three neutered colonies,

two free-ranging and one indoor, detected five main groupings: contact including allogroom, rubbing, aggressive, defensive, and play (Figure 5.7); sexual and maternal behaviour were inevitably not included in these groups. The vertically-raised tail (TU) was associated with both the contact and rubbing groups. In three colonies of entire females, groups of offensive, defensive and contact (including allogrooming) patterns were detected; allorubbing was grouped with sexual behaviour (rolling, lordosis) (van den Bos & de Vries, 1996) (Table 5.2).

These groupings are likely to be affected by the age, sex and reproductive status of the individual cat. They may also be affected by genetics and early experience; the signalling patterns used by McCune (1995) in measuring cats' reactions to familiar and unfamiliar people (see Chapter 4) show some differential effects of paternity (genetics) and early socialisation. Of the defensive vocalisations (directed towards a person), growl was inhibited by socialisation but unaffected by paternity, whereas hiss showed stronger paternal effects. The frequency of TU was highest in both friendly-fathered and socialised cats, but purring was not affected by paternity, and only enhanced by socialisation in the presence of a familiar person.

Communication in the undomesticated felids: the effect of domestication on signalling behaviour

Given the small number of generations since domestication, it is reasonable to assume that the domestic cat's repertoire of signals is largely unchanged from that of its direct ancestor, the African wildcat *F. s. libyca*. However, domestication has substantially increased the requirement for social communication, both intra- and interspecific. It should therefore be possible to investigate the effect of domestication on communication behaviour through a comparison of signalling in the domestic cat with that of undomesticated felids.

Phylogeny of the Felidae

Current ideas on the phylogeny of the Felidae are largely based upon molecular techniques, including albumin immunological distance (Collier & O'Brien, 1985) and isozyme genetic distance (O'Brien *et al*, 1987) (for review see Wayne *et al*., 1989) and mitochondrial gene sequence analysis (Masuda *et al*., 1996), as well as the morphology of skulls (Werdelin, 1983). Three major lineages are thought to exist (Figure 5.8): the ocelot lineage, which includes the small South American cats; the domestic cat lineage, which includes the small Mediterranean cats; and the pantherine lineage, made up of large and small cats from several continents.

Spatial organisation in undomesticated Felidae

Both the function of a signal and the modality employed are highly dependent on the distance between the emitter and the receiver. Communication is therefore intimately related to spatial organisation. For any predator feeding on sparsely distributed small prey, non-overlapping hunting areas are predicted (Ewer, 1973; Kleiman & Eisenberg, 1973; Milinski & Parker, 1991). Field studies have shown this to be the case for most wild undomesticated cats, including *Felis silvestris* (*F. s. silvestris*: Corbett, 1979, Stahl, Artois & Aubert, 1988; *F. s. libyca*: Fuller, Biknevicius & Kat, 1988). There are three notable exceptions: the lion *Panthera leo* (Schaller, 1972), the cheetah *Acinonyx jubatus* (Eaton, 1970; Caro & Collins, 1987; Caro, 1989), and the domestic cat (see Chapter 7), all of which have been found living gregariously. The domestic cat is, however, by no means an obligate group-living species, and has been frequently documented to be solitary when food is at low density and sparsely distributed (Chapter 7). Group-living is most often triggered by an artificial clumping of food associated with human settlements. The change in niche caused by domestication may therefore cause a decrease in the adaptive value of solitary life, and a corresponding change in intraspecific communication.

Communication in the undomesticated Felidae; differences between lineages

Even in solitary species or individuals, signalling is necessary for mating, parent–young interactions, and maintenance of territorial boundaries. The wide range of signals exhibited by these largely solitary animals is demonstrated by the ethograms in Tables 5.3 and 5.4; most species have been found to exhibit a rich repertoire of signals despite being predominantly solitary. However, the frequently nocturnal and solitary behaviour of these species hinders the study of communication, and as a result much of the published

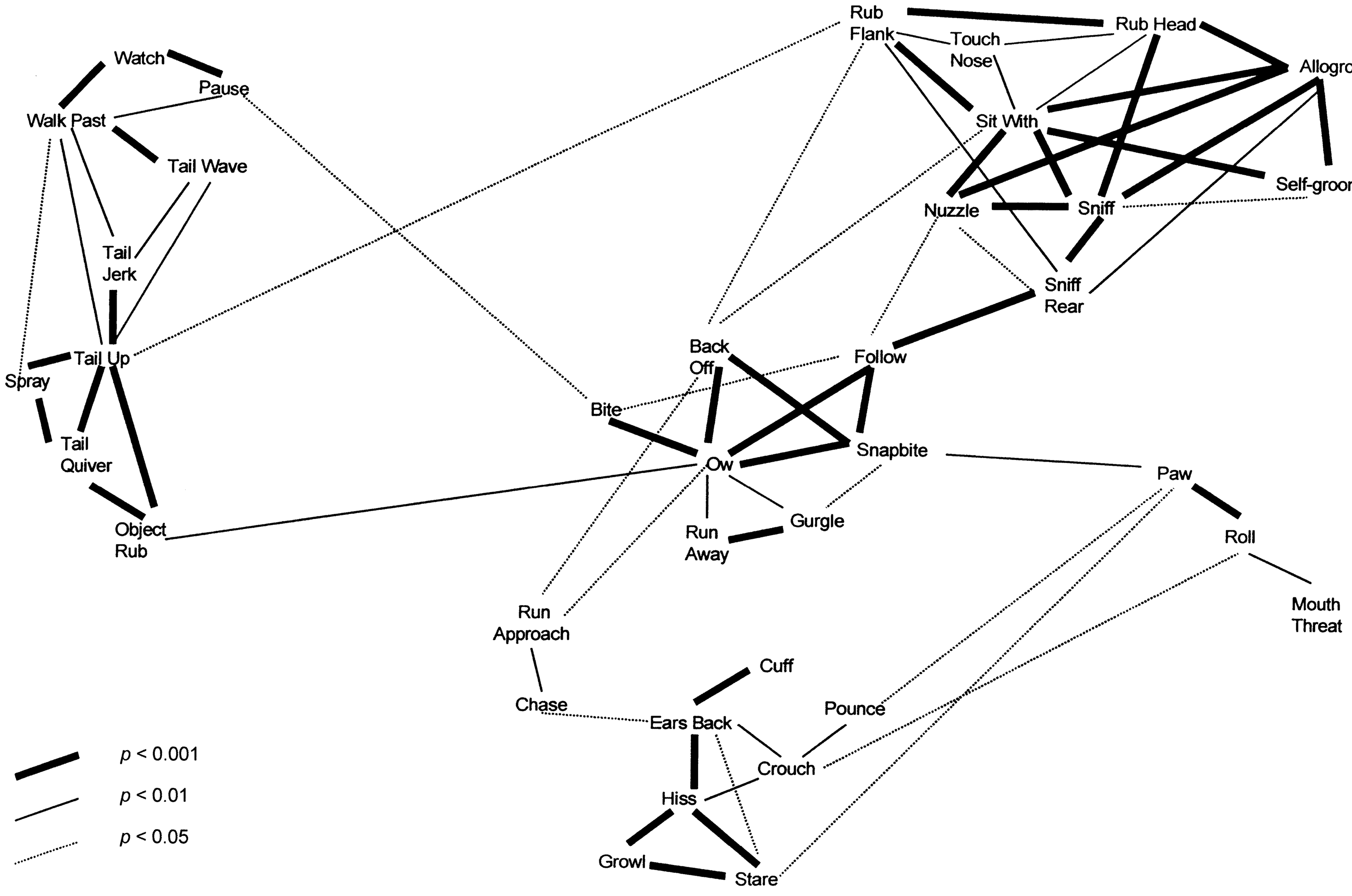


Figure 5.7. Significant links between behaviour patterns performed by the same cat during a single interaction, calculated from adjusted residuals from chi-squared tests. Based on pooled data from 2044 interactions observed by Brown (1993) in three colonies ($n = 26, 11, 5$) of neutered adult cats. Patterns that were observed but not included because they occurred in fewer than 10 interactions were: Arch Back, Growl, Mount, Fight. From Cameron-Beaumont (1997).

Table 5.2. *Groupings of behaviour patterns performed in three confined colonies of entire females (n = 10, 10, 9)*

Colony	A					B					C				
Factor	F1	F2	F4	F3	F5	F2	F1	F5	F4	F3	F2	F1	F3	F5	F4
Rolling	91					XX	XX	XX	XX	XX	XX	XX	XX	XX	XX
Lordosis	84					87					90				
Rubbing	83					62					83				
Biting	–	–	–	–	–	75							95		
Grooming		74				83						46	69		
Sniffing		86				62	42					83			
Nosing			93			82						78			
Sniff rear		66	46				90								64
Treading	–	–	–	–	–	78						53		56	
Defensive				91				97						88	
Staring				76	48			44	76	XX	XX	XX	XX	XX	XX
Offensive					92				92						75

Figures are percentage factor loadings (values <40 omitted) from separate varimax-rotated factor analyses performed on the patterns exchanged within each pairwise combination of cats in each colony. XX, insufficient data for analysis; –, pattern not included in the ethogram for this group.
From van den Bos & de Vries (1996).

data, particularly on small cats, has been collected on captive individuals.

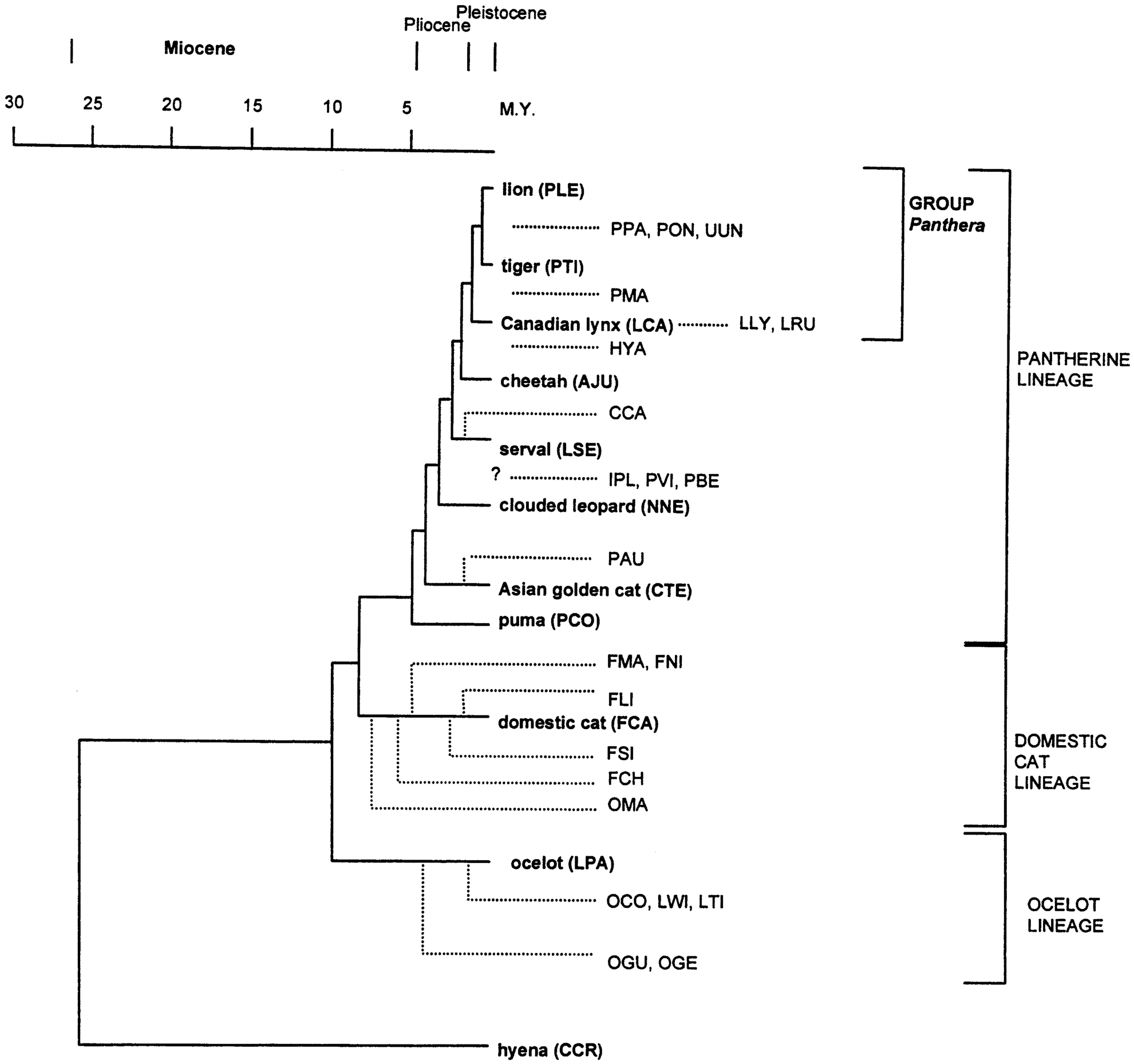
Olfactory communication

Olfactory signals are long-lasting and would therefore be expected to play an important part in communication between both social and solitary members of the Felidae.

Urine
Urine is emitted in the two ways described for the domestic cat, spraying or squat urination. Spraying occurs more frequently in males than in females (Wemmer & Scow, 1977; Mellen, 1993). Sprayed urine has been suggested to contain anal gland secretions, whereas squat urinations appear unlikely to contain any extra components (Schaller, 1972). Squat urinations differ also in that the urine is usually raked into the soil with the hind feet (known as scuffing/scraping or raking). It has been suggested that this action may mix urine into the soil and aid the transfer of urine scent (Verberne & Leyhausen, 1976), and possibly also the scent from the glands on the feet (Wemmer & Scow, 1977) to the environment; however, the communciative function of this behaviour is not known.

Scraping
Undomesticated cats have additionally been documented to scrape their hind feet without urination or defaecation (Hornocker, 1969; Schaller, 1972; Seidensticker *et al.*, 1973; Wemmer & Scow, 1977; Smith, McDougal & Miquelle, 1989). The absence of urine, faeces or anal gland secretions implies that scrapes are acting as visual signals as well as olfactory ones (Smith *et al.*, 1989), although scraping may help to pass secretions from the glands in the feet on to the substrate (Wemmer & Scow, 1977). Seidensticker *et al.* (1973) found that scrapes by mountain lions *Puma concolor* demark home ranges, visually and/or chemically.

Mellen (1993) compared the presence and absence of scraping in 20 species of small cats. Scraping occurred in most of the species that she observed within the ocelot and Panthera lineages, but in only one species within the domestic cat lineage, Pallas's cat (*Otocolobus manul*). This species probably diverged from the remainder of the domestic cat lineage at an early stage (see Figure 5.8), in which case this



AJU Acinonyx jubatus
CCA Caracal caracal
CCR Crocuta crocuta
CTE Catopuma temmincki
FCA Felis silvestris catus
FCH Felis chaus
FLI Felis silvestris lybica
FMA Felis margarita
FNI Felis nigripes
FSI Felis silvestris silvestris
HYA Herpailurus yagouaroundi
IPL Ictailurus planiceps
LCA Lynx canadensis
LLY Lynx lynx
LPA Leopardus pardalis
LRU Lynx rufus
LSE Leptailurus serval
LTI Leopardus tigrina
LWI Leopardus wiedii
NNE Neofelis nebulosa
OCO Oncifelis colocolo
OGE Oncifelis geoffroyi
OGU Oncifelis guigna
OMA Otocolobus manul
PAU Profelis aurata
PBE Prionailurus bengalensis
PCO Puma concolor
PLE Panthera leo
PMA Pardofelis marmorata
PON Panthera onca
PPA Panthera pardus
PTI Panthera tigris
PVI Prionailurus viverrinus
UUN Uncia uncia

Figure 5.8. Evolutionary tree of the Felidae, from Wayne *et al.* (1989). The positions of species in **bold** are based on average reciprocal microcomplement fixation measurements (Sneath & Sokal, 1973, Collier & O'Brien, 1985). The positions of species attached by dotted line are based on albumin immunological distance (Collier & O'Brien, 1985). Systematic names have been altered to match those used in this chapter.

Table 5.3. *Ethogram of olfactory, visual and tactile signals exhibited by adult undomesticated felids (for auditory signals see Table 5.4)*

Behaviour	Description	Sources
Olfactory communication		
Urine spray	Cat directs a jet of urine backwards against some object. The tail is raised vertically and, in some species quivered as the urine is discharged. Spray should be distinguished from squat urination (see below).	Smith *et al.* 1989, Wemmer & Scow 1977, Armstrong 1977, Mellen 1988, 1993, Sokolov *et al.* 1995, Bothma & Leriche 1995, Schaller 1967, 1972
Squat urination	This type of urination occurs in a squatting position, and not against an object. Squat urinations are usually accompanied by a raking/scuffing of the hind feet (see below).	Wemmer & Scow 1977, Caro & Collins 1987
Scuffing/scraping/raking of the hind feet	This is often exhibited during squat urination, but does also occur alone. It may be a method of transferring scent from the glands of the feet to the substrate.	Wemmer & Scow 1977, Seidensticker *et al.* 1973, Schaller 1972, Hornocker 1969, Smith *et al.* 1989, Verberne & Leyhausen 1976
Faeces deposition on landmarks	Cat defaecates on a prominent landmark.	Caro & Collins 1987, Lindemann 1955 (in Wemmer & Scow, 1977)
Object Rub	Cat rubs its body or head and neck along the ground or against an object. This behaviour is also strongly associated with female sexual behaviour as a visual signal.	Foster 1977, Petersen 1977, 1979, Eaton & Velander 1977, Mellen 1988, 1993, Ragni & Possenti 1990, Smith *et al.* 1989, Schaller 1972, Bothma & Leriche 1995, Wemmer & Scow 1977, Cameron-Beaumont, 1997
Tree scratching/claw raking	Cat grips tree trunk with extended forelegs and depressed body, and the claws are then drawn backwards simultaneously or alternately in strokes of variable length and speed. This action serves to remove loose claw sheaths but also leaves a visual and possibly olfactory trace (from Wemmer & Scow, 1977).	Petersen 1979, Mellen 1993, Wemmer & Scow 1977, Hornocker 1969, Smith *et al.* 1989, Bothma & Leriche 1995, Schaller 1967, 1972, Seidensticker *et al.* 1973, Eaton 1970
Visual communication		
Watch	One cat idly observes another cat or human. This can be distinguished by the way in which the cat's eye and head movements track what it is watching. This is not necessarily directed at another cat's eyes (which distinguishes it from Stare).	Cameron-Beaumont 1997
Stare	This is similar to Watch, but involves a more fixed stare, with the cat not being easily distracted by any other activity around it. It is often directed at the other cats eyes, and may frequently be followed by the recipient cat looking away.	Bennett & Mellen 1983, Mellen 1993, Cameron-Beaumont 1997
Ears back	Ears are held at the rear of the head.	Cameron-Beaumont 1997

Table 5.3. *continued*

Ears flat	A cat flattens its ears to its head, such that they tend to lie flush with the top of the head.	Petersen 1979, Cameron-Beaumont 1997
Tail Quiver	Tail is held upright and the entire tail is quivered rapidly from the base to the tip of the tail.	Ragni & Possenti 1990
Social Roll	A cat rolls on the ground in the presence of another cat.	Freeman 1983, Foster 1977, Petersen 1977, Ragni & Possenti 1990, Mellen 1993, Cameron-Beaumont 1997
Tail Under	The tail is tucked right under the body. This position is normally held whilst the cat is crouching in a defensive manner.	Cameron-Beaumont 1997
Crouch	The cat crouches in a defensive manner. Cats also often sit in a crouching position. This is not included as being crouching.	Petersen, 1979, Cameron-Beaumont 1997
Lordosis	A female cat crouches down and raises her hindquarters to present her genitals to a male when in a receptive oestrous state. Her tail is turned aside and her belly pressed close to the ground.	Mellen 1993, Cameron-Beaumont 1997
Follow	One cat travels closely behind another.	Foster 1977, Eaton & Velander 1977, Mellen 1988, 1993, Cameron-Beaumont 1997
Knead/Tread	Cat pummels paws into object or ground in a kneading motion. Claws may be in or out. May occur with either the front or back feet. Treading (also called skating) of the back feet is particularly associated with the female during reproduction.	Foster 1977, Petersen 1977, Ragni & Possenti 1990
Arch back	A cat curves its back upwards and stands rigidly. The tail is usually tensely curved and the fur may be piloerected.	Cameron-Beaumont 1997
Mouth threat	Cat gapes its mouth and puts its ears back in the expression that would normally be attributed to a hiss, but no sound is made.	Cameron-Beaumont 1997
Snapbite	Cat opens its mouth and snaps it shut, as if biting the air. This is normally directed towards another cat.	Cameron-Beaumont 1997
Social Rub	Cat rubs another cat (see Macdonald *et al.* 1987). Subdivisions include: Rub head (one cat rubs its head on another), Rub flank (one cat rubs its flank on another), and Rub tail: (one cat rubs its tail on another).	Petersen 1979, Mellen 1993, Cameron-Beaumont 1997, Ragni & Possenti 1990, Schaller 1972, Wemmer & Scow 1977
Social grooming or allogrooming or social licking	One cat licks another cat.	Petersen 1977, 1979, Bennett & Mellen 1983, Mellen 1993, Cameron-Beaumont 1997, Freeman 1977, Foster 1977, Schaller 1972

Pounce	Cat leaps at or on to another cat.	Cameron-Beaumont 1997
Social Play	Social play has been divided into contact social play, and non-contact social play by Caro (1995). The various behavioural elements involved in this are described in this paper. Contact social play has also been described as jostle play (described as: one cat struggles with another cat, raking with its hind legs and pulling the opponent towards its body with its forepaws).	Petersen 1979, Cameron-Beaumont 1997, Bennett & Mellen 1983, Caro 1995
Sniff Cat	One cat smells the body of another cat. It may be subdivided into: Sniff Nose (two cats sniff each other's noses), Sniff Rear (one cat smells the peri-anal area of another cat), and Sniff Body (one cat smells the head, flank or tail of another cat).	Mellen 1988, 1993, Cameron-Beaumont 1997, Freeman 1983, Petersen 1977, Eaton & Velander 1977, Wemmer & Scow, 1977
Touch Nose	Two cats touch each other's noses; this is probably accompanied by Sniff Nose	Cameron-Beaumont 1997, Petersen 1979
Mount	One cat attempts, but fails to achieve, intromission. The mounting cat normally holds the recipient firmly at the nape of the neck whilst mounting (see Nape Bite). It is also sometimes accompanied by treading movements of the hind legs.	Bennett & Mellen 1983, Mellen 1988, 1993, Petersen 1977, 1979
Nuzzle	One cat pushes its head against the head or, more uncommonly, the body of another cat. This resembles the form of a brief Rub but there is no rubbing action, only a gentle push.	Cameron-Beaumont 1997
Paw/pat	One cat pats another individual with its forepaw, keeping claws retracted.	Foster 1977, Mellen 1993, Wemmer & Scow 1977, Cameron-Beaumont 1997
Bite	One cat snaps its teeth at or succeeds in nipping another animal.	Mellen 1993, Wemmer & Scow 1977, Cameron-Beaumont 1997
Nape bite	The hold used by the male cat whilst mounting the female. The female's neck is held in a firm bite-hold.	Mellen 1993
Cuff	One cat strikes another cat with its forepaw, usually with claws extended.	Mellen 1988, 1993, Bennett & Mellen 1983, Cameron-Beaumont 1997
Sit With	A cat sits next to, or very near to, another cat.	Bennett & Mellen 1983, Cameron-Beaumont 1997

Signalling behaviour in undomesticated felids has been discussed by various authors, but without a definitive ethogram, although one has been collated for the domestic cat (UK Cat Behaviour Working Group, 1995). Many of the behaviours described are similar to those of the domestic cat. Descriptions are based on the references given in the third column.

Table 5.4. *Calls and sounds of the Felidae; lineage differences*

Call	Domestic cat lineage	Pantherine lineage	Ocelot lineage
Purr	FSI (Ragni & Possenti 1990), FNI (Armstrong 1977)	PLE (Schaller 1972), CCA (Peters 1983), *Lynx* sp. (Peters 1987)	LWI (Petersen 1979)
Meiow	FSO (Cameron-Beaumont 1997)	CCA (Peters 1983; Cameron-Beaumont 1997), *Lynx* sp. (Peters 1987)	LWI (Petersen 1979)
Growl	FMA, FCH, FNI, FCA (Mellen 1993)	CCA (Peters 1983), *Lynx* sp. (Peters 1987), CTE, PRU, LSE, CCA, PAU, HYA, Siberian lynx (Mellen 1993), PLE (Schaller 1972)	LWI (Petersen 1977, 1979), OGE (Mellen 1993, Cameron-Beaumont 1997), LPA (Mellen 1993)
Yowl	FCH (Cameron-Beaumont 1997)	*Lynx* sp. (Peters 1987)	OGE (Cameron-Beaumont 1997)
Snarl		PLE (Schaller 1972)	LWI (Petersen 1979)
Hiss	FNI (Armstrong 1977), FMA (Bennett & Mellen 1983), FMA, FCH, FNI, FCA (Mellen 1993)	CCA (Peters 1983), *Lynx* sp. (Peters 1987), PVI, CTE, PRU, LSE, CCA, PAU, HYA, LCA (Mellen 1993), PLE (Schaller 1972)	LWI (Petersen 1979), OGE, LPA, OCO, (Mellen 1993)
Spit	FNI (Armstrong 1977), FMA, FNI, FCA (Mellen 1993)	CCA (Peters 1983), *Lynx* sp. (Peters 1987), PLE (Schaller 1972)	LWI (Petersen 1979), OCO (Mellen 1993)
Gurgle	FSI, FSO, FCA, FCH, FMA, FNI (Peters 1984b)	PBE, PRU, PAU, CTE, PCO, CCA, HYA, LSE, PMA,LLY, LRU, AJU (Peters 1984b), CCA (Peters 1983), *Lynx* sp. (Peters 1987)	LPA, LTI, OGE, (Peters 1984b).
Puffing	X	PPA, PLE (Peters 1984b), PLE (Schaller 1972)	X
Prusten	X	NNE, UUN, PTI, PON (Peters 1984a, b)	X
Wah-wah	?	CCA (Peters 1983), *Lynx* sp. (Peters 1987)	?
Chatter	FSI (Ragni & Possenti 1990)	*Lynx* sp. (Peters 1987)	
Male sexual advertisement call during courtship[a]	FSI (Ragni & Possenti 1990), FMA (Hemmer 1976: bark)	AJU (Foster 1977: eeow), UUN (Peters 1982, Rieger & Peters 1981)	LWI (Petersen 1977: barking meow or yelp, trilling meow)
Female sexual advertisement call during courtship[a]	FSI (Ragni & Possenti 1990: cry)	AJU (Foster 1977: eeow), PTI (Kleiman 1974), CCA, PVI, UUN (Seager & Demorest 1978)	LWI (Petersen 1977: barking meow)
Female copulatory			LWI (Petersen 1977)
Roar	X	PLE (Schaller 1972)	X

X, Stated to be absent in that lineage;

?, May be absent in that lineage.

[a] No uniform name is given to the male and female's sexual advertisement call, probably because the actual sound varies between species. The name given to the call in each species is therefore given after the author in each case.

For key to species see Fig. 5.8, except: FSO = *Felis silvestris ornata*, PRU = *Prionailurus rubiginosus*.

behaviour may imply an evolutionary loss/change amongst an ancestral member of the domestic cat lineage. Wemmer & Scow (1977) similarly found that this behaviour was absent in the genus *Felis* (used in the strict sense to mean only cats in the same lineage as the domestic cat).

Faeces deposition

The method of faeces deposition varies according to species (reviewed in Wemmer & Scow, 1977). However, it is difficult to see if there is an evolutionary pattern to these differences or whether they are dependent on local conditions. Lindemann (1955, in Wemmer & Scow, 1977), found that the Canadian lynx (*Lynx canadensis*) and the European wildcat (*F. s. silvestris*) used two methods, dependent on where the defaecation took place; faeces were localised and covered within territories, but left uncovered in prominent positions at points between territories (which were used as mating rendezvous sites in the lynx). This finding suggests that the method of defaecation may depend on local conditions rather than on phylogeny.

Skin glands

As for the domestic cat, tree-scratching functions to remove loose claw sheaths (Wemmer & Scow, 1977), but it is also used as part of the scent-marking routine in most cats, often occurring in the same areas as other methods of scent-marking (Mellen, 1993). It may also leave a visual signal (Wemmer & Scow, 1977). This behaviour occurs in a diverse range of felids (Pallas's cat, sand cat, fishing cat, Temminck's golden cat, jungle cat, rusty spotted cat, Indian desert cat, serval, caracal, African golden cat, Geoffroy's cat, jaguarundi, ocelot, Scottish wildcat, Siberian lynx, Canadian lynx: Mellen, 1993; margay: Petersen, 1979; tiger: Schaller, 1967, Smith *et al.*, 1989; lion: Schaller, 1972; Canadian lynx, Pallas's cat, jaguar, fishing cat, leopard cat: Wemmer & Scow, 1977; snow leopard: Hornocker, 1969; Seidensticker *et al.*, 1973; cheetah: Eaton, 1970; leopard: Bothma & Leriche, 1995), and appears to have changed little in character or function during the course of felid evolution.

Object-rubbing has been suggested to have three ways of acting: first, it acts as a method of scent-marking by depositing gland secretions such as saliva on objects (Ewer, 1973; Wemmer & Scow, 1977). Rieger & Walzthony (1979; see also Rieger, 1979) additionally suggest that object-rubbing picks up scent, as many species of small felids rub on objects previously sprayed with urine (Wemmer & Scow, 1977). Both of these theories were supported by Mellen's (1993) data in which scents were seen being both picked up (*e.g.* urine) and deposited (e.g. saliva) by a variety of species. Thirdly, observations from many species suggest that object-rubbing acts as a visual signal during reproductive and oestrous behaviour (*Acinonyx jubatus*: Foster, 1977; *Leopardus wiedii:* Petersen, 1977; *Puma concolor*: Eaton & Velander, 1977; *F. s. silvestris*: Ragni & Possenti, 1990; *Oncifelis geoffroyi*: Cameron-Beaumont, 1997) and in many species of small cats (Mellen, 1993), as it does in the domestic cat (Rosenblatt & Aronson, 1958; Michael, 1961). Taken together, these observations suggest that all three lineages of undomesticated cats use object-rubbing similarly, as a signal of both visual and olfactory nature.

The function of scent-marking was investigated in tigers (*Panthera tigris*) by Smith *et al.* (1989), who proposed that it plays a role in establishing and maintaining territories. They found that scent-marking was concentrated at potential contact zones where major routes of travel approached territorial borders, which supported the hypothesis that the density and age of scent-marks give invaders some information about the probability of encountering another animal, and therefore also about its risk of injury by being in that area. This fits with the oft-cited observation that scent-marks rarely act as an immediate deterrent to invaders (Leyhausen, 1965; Schaller 1972; Mellen, 1993). Previous hypotheses on the function of scent-marking have tended to involve the idea that this behaviour provides temporal information about the whereabouts of each individual cat (Leyhausen, 1965; Schaller, 1967, 1972; Hornocker, 1969; de Boer, 1977), which may also be the case, although as noted above, the benefit to the producer of the signal is unclear. The second function of scent-marking found by Smith *et al.* was that it serves to signal the onset of oestrus in the female. This was supported by Mellen (1993), who found that a change in the marking rate of the female was a good indicator of reproduction in a variety of small cat species.

Acoustic communication

Acoustic signals in felids carry a wide variety of messages (Peters & Wozencraft, 1989), and are used across long distances as well as during close contact and in group-living felids as well as solitary ones. For

example, calls can display territorial advertisement (Eisenberg & Lockhart, 1972), defensive and offensive threat (spit, hiss, growl, snarl: Wemmer & Scow, 1977; Peters, 1983; Cameron-Beaumont, 1997), close range affiliation (prusten, gurgle, puffing: Peters, 1984a, b), mating signals, both for sexual advertisement (male and female sexual calls: Kleiman, 1974; Foster, 1977; Petersen, 1977; Seager & Demorest, 1978; Peters, 1980; Rieger & Peters, 1981; Ragni & Possenti, 1990) and during copulation (Peters, 1978; Rieger & Peters, 1981), infant signals of contact (purr, miaow: Schaller, 1972) and distress (miaow); identification messages (call sequence duration in lions: Peters, 1978); and to encourage assembly of a group (roaring of lions: Schaller, 1972). Table 5.4 lists the most commonly cited calls, and those which have been described in some detail.

Unfortunately, however, it is impossible to create an exhaustive ethogram of felid calls because detailed information on many species is sparse. There are anecdotal mentions of other sounds (e.g. Schaller, 1972; Foster, 1977; Petersen, 1979; Cameron-Beaumont, 1997) but it is not usually possible to tell whether these are distinct sounds or just a grading of a previously recorded call, or a slight call variation between species. For the well-detailed or well-known calls listed in Table 5.4, however, most appear to be relatively uniform across the three lineages, although the roar is found only in the Panthera lineage. Other differences include the close-range friendly affiliation call described by Peters (1984a, b), which differs in structure across the three lineages, there being three types (gurgle, prusten and puffing), all of which are thought to have the same function in different species. Threat and infant sounds appear to be relatively uniform. The less commonly cited calls include the wah-wah and the chatter, both described by Peters (1983, 1987). It is not known how widespread these two sounds are across the lineages.

Visual communication

As in domestic cats, social rolling in undomesticated felids is a component of sexual behaviour (*Uncia uncia*: Freeman, 1983; *A. jubatus*: Foster, 1977; *L. wiedii*: Petersen, 1977; *F. s. silvestris*: Ragni & Possenti, 1990; several species, Mellen, 1993), although in captive cats it does also occur in general social situations (*O. geoffroyi*, *F. chaus*, *Caracal caracal*: Cameron-Beaumont, 1997). There is, however, no evidence of social rolling in undomesticated felids being used in the submissive manner described for the domestic cat.

With the exception of Tail Under, which occurs in conjunction with Crouch as a defensive posture, no other tail position appears to act as a signal in undomesticated cats (Cameron-Beaumont, 1997). The one exception is the lion, which has been reported to show a Tail Up position in conjunction with rubbing, although it was not described as a signal (Schaller, 1972); this is discussed further in the section on effects of domestication (p. 87).

There has been no investigation into the use of body and face signals in undomesticated felids, with the exception of Schaller (1972), who describes the use of these visual signals in the lion.

Tactile communication

Tactile communication in free-ranging solitary felids generally occurs as a component of either mating or mother–young behaviour. However, in zoos (where unrelated adult cats are often kept together), tactile communication between adult cats is regularly observed in a more general social context, although the rates of tactile contact vary. Many naturally solitary cats have been observed to be sociably tactile in captivity (Mellen, 1993; Cameron-Beaumont, 1997), which demonstrates the felids' ability to adapt their behaviour according to the prevalent conditions, although other captive studies have found low rates of tactile contact (Tonkin & Kohler, 1981; Bennett & Mellen, 1983). The rate appears to depend on individuals rather than on the species involved.

In social cats, particularly the lion and the domestic cat, tactile signals are frequently used as general social signals as well as more specifically in a reproductive or parental context. Interestingly, tactile signals appear to be used in a similar manner in these two social species, despite their different evolutionary lineages.

Social rubbing amongst small felids has not been documented in the wild; in captivity, it may be derived from the mating ritual, due to its occurrence during reproductive behaviour (*F. s. silvestris*: Ragni & Possenti, 1990; *P. leo*: Schaller, 1972; *O. geoffroyi*: Cameron-Beaumont, 1997; several species of small cats: Mellen, 1993). However, some publications on felid reproductive behaviour do not mention social rubbing, despite mentioning object-rubbing (*A. jubatus*: Foster, 1977; *P. concolor*: Eaton & Velander, 1977).

Social rubbing amongst lions has been reported in more detail, occurring as an affiliative behaviour between adults. Schaller (1972) found that rubbing occurred particularly after members of the group had been separated, and also after agonistic interactions. He suggested that this behaviour indicates that the intentions of the animal are peaceful. He found that males rarely rubbed on females or cubs, while females rubbed on both males and females, and cubs rubbed mostly on females; this is compatible with the explanation that rubbing acts as a placatory gesture, producing more benefit for a subordinate animal than for a dominant. Interestingly, this system has also been proposed for the other group-living cat, the domestic cat (Macdonald *et al.*, 1987). The fact that both lions (Panthera lineage) and domestic cats (domestic cat lineage) appear to use social rubbing as a placatory signal implies that rubbing may have a similar function in mating behaviour amongst solitary cats, i.e. indicating that the intentions of the animal are peaceful, both before and after copulation. If this is the case, then it is understandable that this signal has diversified to be used in other social contexts amongst the two gregarious species, *F. s. catus* and *P. leo*, despite their different lineages.

Social grooming in solitary cats occurs both as part of mating behaviour (Schaller, 1972; Foster, 1977; Freeman, 1977; Petersen, 1977; Cameron-Beaumont, 1997) and in mother–young interactions, in which it has a utilitarian function of maintaining the cubs' cleanliness. In the gregarious lion it occurs in these two situations, and additionally in a non-specific social situation, frequently when two are resting together (Schaller, 1972). The function of this has not been elucidated. Normally solitary cats kept in captivity also use social grooming in this non-specific manner (Mellen, 1993; Cameron-Beaumont, 1997).

The effect of domestication on cat–cat signalling behaviour

During domestication *F. silvestris* must have adapted to living at higher densities than previously, and then subsequently adopted group-living. Since the signals needed by solitary animals have different properties from those needed by group-living individuals, this move may have led to an evolutionary change in the signalling patterns used by this species.

Signals must be derived originally from non-signal movements, by ritualisation (Harper, 1991). Further ritualisation can then occur, whereby a signal diversifies, giving rise to several functionally distinct signals, via the following stages:

1 Signal occurs in one context only.
2 Signal appears in two contexts, assuming a second function, but remains structurally unchanged.
3 The two signals become structurally distinct in the two contexts.

Stage 2 is therefore an essentially transient phase between Stages 1 and 3 (Otte, 1974).

Domestication can provide an insight into the process of ritualisation of signals, because it is possible to compare the domestic cat with relatives that behave very similarly to its ancestor; thus it is possible to determine whether any diversification or ritualisation of signals has occurred during domestication. Differences between signals used by the domestic cat and undomesticated felids are therefore discussed below, these being differences which may have been caused by domestication, both by altering the circumstances in which intraspecific behaviour is expressed (e.g. high local population densities), and by introducing a need for interspecific (i.e. cat–human) communication.

(1) The evolution of a new signal from a non-signal behaviour: Tail Up

The action of Tail Up, as an integrative part of urine-spraying, is thought to occur in all species of felids, domestic and undomesticated. The tail is raised vertically during spraying and then immediately lowered (Hornocker, 1969; Schaller, 1972; Wemmer & Scow, 1977; Smith *et al.*, 1989; Mellen, 1993; Bothma & Leriche, 1995; Solokov, Naidenko & Serbenyuk 1995). However, in domestic cats, Tail Up has additionally been shown to act as an affiliative signal (Cameron-Beaumont, 1997). The Tail Up affiliative signal differs from the raised tail that occurs during urine-spraying in both context (being linked to affiliative behaviours, in particular social rubbing) and structure (occurring for prolonged periods of time, often remaining upright during locomotion) (Cameron-Beaumont, 1997).

Cameron-Beaumont (1997) investigated the point at which the Tail Up affiliative signal might have evolved by looking for its presence in undomesticated felids, using representatives from all three evolution-

ary lineages. There was no evidence of its presence in any of the three species studied (*O. geoffroyi* (ocelot lineage), $n = 14$; *C. caracal* (Panthera lineage), $n = 13$; *F. chaus* (domestic cat lineage), $n = 12$) during a total of 539 hours of observation. All three species carried out social and object rubbing without raising their tail; this is in contrast to domestic cats, where rubbing is almost exclusively carried out with the tail held vertical. The raised tail during spraying was, in contrast, observed in all species. None of the publications which discuss felid communication and behaviour (with the exception of the lion: see below) mention Tail Up occurring in any context other than urine-spraying (Wemmer & Scow, 1977; Mellen, 1993; Table 5.3).

This study appears to suggest that Tail Up may have evolved as an affiliative signal during domestication, perhaps consecutively with increased sociality, which may have caused the necessity of an additional visual signal. However, it cannot be ruled out that the Tail Up signal may have evolved at an earlier stage, possibly amongst one of the undomesticated forms of *F. silvestris*. There are few behavioural studies on the undomesticated subspecies of *F. silvestris*, particularly the African subspecies, which may account for the absence of any mention of Tail Up.

The one exception to this is Schaller's description of social behaviour in lions (*Panthera leo*), in which he states that social rubbing (in both mating and general social situations) frequently occurs with the tail raised. He writes: 'During head-rubbing and anal-sniffing contacts the animals raise their tail so that it either arches over their back or tips towards the other animal.' He gives no more detail about the contextual nature of this behaviour, but the fact that it occurs with the affiliative behaviours of rubbing and anal sniffing implies that it is being used in a different way from the raised tail during spraying. Its function in lions may even be similar to that in domestic cats (i.e. as an affiliative signal). The occurrence of a Tail Up affiliative signal only in *F. s. catus* and *P. leo*, from different evolutionary lineages, but not in any other undomesticated species of felid, implies that this signal may have evolved separately in the two species, possibly as a result of similar selective pressures acting only on the two most social species of cats.

Various previous investigations have looked for the emergence of a new behavioural pattern as a result of domestication (reviewed in Kruska, 1988), but to date no new behaviours have been found, despite many quantitative differences in the character of signals. Thus it would prove particularly interesting if the Tail Up affiliative signal is found to have evolved as a result of domestication.

(2) An established signal diversifies to develop a secondary function (i.e. occurs in a new context), but does not change in structure

Social rolling in undomesticated felids is a sexual signal, occurring as part of the reproductive repertoire. In domestic cats it is still used in this reproductive manner (Rosenblatt & Aronson, 1958; Michael, 1961), but is additionally used as a submissive gesture in groups of domestic cats (Feldman, 1994b). There is no evidence that undomesticated felids use social rolling for this function, although it is possible that its role in sexual behaviour is a submissive one, in which case it is only a small step to its general (non-sexual) use as a submissive behaviour in groups of domestic cats.

Social rubbing and social grooming are also both sexual signals in undomesticated felids. In the domestic cat, however, they are additionally used in a general social greeting situation. However, this change in context and thus in function cannot be attributed to domestication, because adult undomesticated cats in zoos exhibit the same changes, i.e. an increased use of head-rubbing and grooming in non-sexual situations (Cameron-Beaumont, 1997). Thus the use of these behaviours in a wide variety of affiliative contexts is probably a natural ability of all felids rather than a product of domestication.

Neotenised signals

Miaow, knead and purr are all generally considered to be juvenile behaviours, with the possible exception of purr, which also occurs in adult cats (Peters, 1981). However, in the cat–human relationship, adult cats use all three of these signals habitually (e.g. Turner, 1991; Bradshaw & Cook, 1996). Cameron-Beaumont (1997), in a survey of zoo keepers, found that adult undomesticated cats in captivity were very unlikely to perform any of these three vocalisations towards humans, suggesting that undomesticated cats cannot naturally revert to performing kitten behaviours when adult. This discrepancy suggests that the domestic cat has evolved (either culturally or genetically) the ability to use kitten behaviours towards humans when adult (neoteny).

(3) An established signal diversifies in both structure and function to become a different signal

There are no definite examples of this in the cat–cat relationship, but a change in signal structure does appear to have occurred in cat–human signals.

Cameron-Beaumont (1997) investigated the use of rubbing in the domestic cat in both cat–cat interactions and in cat–human interactions. In the human-directed situation, rubbing occurs at a higher frequency and at a higher intensity than it does in the cat–cat situation. This difference is likely to have occurred partly because of the change in receiver psychology (Guilford & Dawkins, 1991), but also because of the change in the meaning of the signal; it is likely that much of human-directed cat behaviour is exhibited as either a food- or attention-getting signal (see also Mertens & Turner, 1988). This is in contrast to the message given in the cat–cat situation (where it acts as a subtle affiliative signal). A food-eliciting signal would favour a 'loud' prominent signal, whereas an affiliative cooperative signal between members of a colony would favour a subtle cue (Krebs & Dawkins, 1984). Thus the difference in the type of message that is being given by rubbing may cause a difference in the frequency and intensity with which the signal is given. This ritualisation of an established cat–cat signal in the cat–human situation may have also occurred in other common cat–human signals such as the miaow.

Concluding remarks

Despite a substantial literature on communication in the cat family, several important issues remain to be resolved. The first is whether everything that has been described as communication really involves transmission of information from one cat to another, and conversely, whether all the signals produced by the domestic cat have been identified. Most signals have been defined on the basis that they are behaviour patterns that are obvious (to humans) and which appear to elicit responses from other cats. However, rigorous interpretation of a behaviour pattern as a signal requires that it should be tested independently of the context in which it normally occurs. This is more easily achieved for vocal signals (playback experiments) and chemical signals (presentation of isolated or synthetic odours) than for visual or tactile cues, where the signal is difficult to separate from the animal as a whole, although Cameron-Beaumont (1997) has achieved it for the Tail Up posture.

There is also a possibility that the domestic cat produces subtle signals which have yet to be identified as such. Cooperative signals may be very difficult to detect experimentally, since they should be produced with the minimum amount of energy required, and should keep the signaller as inconspicuous as possible to minimise detection by predators (Krebs & Dawkins, 1984). For example, the grunts emitted by vervet monkeys, although indistinguishable to the human ear, are produced in at least two distinct forms with different meanings (Cheney & Seyfarth 1982). Since sociality in the domestic cat may be somewhat primitive, and may even have evolved as a consequence of cats' association with humans, we might not expect such signals to have emerged as yet. However, this may be something of a circular argument, i.e. we may regard the cat's social system as primitive because we have not yet identified all the signals by which relationships are established and maintained, and also do not yet fully understand those we have identified.

It is still unclear, for example, whether conventional concepts of 'dominance', which are so useful in interpreting the social behaviour of other species, can be usefully applied to the cat. In terms of signals, the roles of allogrooming and rubbing in redirecting and averting aggression warrant further investigation.

Our understanding of the role of scent-signals in social behaviour has also lagged behind that of some other mammals, particularly since synthetic analogues of the so-called 'facial pheromones' of the cat are now becoming commercially available for the control of indoor urination (White & Mills, 1997) and aggressive behaviour (Pageat & Tessier, 1998). All of the scent-marking performed by cats is in need of reappraisal in terms of the benefits accrued by the depositor, as well as the recipient, as we have attempted to do for spray-urination by males.

Finally, the cat offers considerable opportunities to examine the effects of domestication on signalling. This may have occurred in two non-exclusive ways: either 'hard-wired' changes in the structure and/or meaning of signals which are inherited genetically, or an enhanced ability to learn to communicate in new ways, particularly when signalling to humans. We suggest that the appearance of the Tail Up signal is an example of the former, appearing as a method for avoiding unnecessary conflict as cats adapted to

living in high densities around human habitations. Neotenisation may have extended the use of some signals, particularly vocalisations, from the juvenile stage to the adult. Other signals, most notably the miaows, since they vary considerably in form from one individual to another, may reflect an increased plasticity in performance, enabling the development of an interspecific as well as an intraspecific repertoire.

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