

NORMAL FELINE BEHAVIOUR ... and why problem behaviours develop

John Bradshaw

Introduction

Clinicians have been describing and classifying cats' problematic behaviours for several decades, but everyday relationships between cats and their owners remain remarkably undocumented. As a species, domestic cats have been the subject of many behavioural and ecological studies,¹ but often as proxies for other, less accessible carnivores, or, more recently, because conservationists perceive their predatory instincts as damaging to wildlife,² so the relevance of these studies to clinical practice can only be inferential. Because they live literally under the noses of their doting owners, it is easy to imagine that the behaviour of pet cats presents no mysteries; but, until recently, science has paid very little attention to how cats relate to the very surroundings in which most behavioural disorders become apparent – the home, and its human and animal occupants. Classification and diagnosis of these disorders has therefore

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come to be based upon a mixture of:

- ✦ Comparisons with other species (most practitioners treat more dogs than cats);
- ✦ Custom and conjecture (as there has been so little published research, most writings on feline behaviour problems are unavoidably a rehash of what has gone before);
- ✦ Common-sense extrapolations from what is known about feline cognition and cat–cat social behaviour. It is this last category that forms the basis of this review.

SERIES OUTLINE

This article forms part of a series of evidence-based reviews on feline behaviour, independently written by key opinion leaders, spanning three Special Issues of *JFMS*. An outline of the series is included as supplementary material alongside the article at: cpsj.jfms.com



Practical relevance: Cats are descended from a solitary, territorial ancestor, and while domestication has reduced their inherited tendency to be antagonistic towards all animals larger than their typical prey, they still place more reliance on the security of their territory than on psychological attachments to people or other cats, the exact opposite to dogs. Many feline problem behaviours stem from perceived threats to this security, often due to conflicts with other cats. Others are more developmental in origin, often caused by inadequate exposure to crucial stimuli, especially people, during the socialisation period. Strongly aversive events experienced at any age can also contribute. A third category comprises normal behaviour that owners deem unacceptable, such as scratching of furniture.

Evidence base: This review identifies three areas in which basic research is inadequate to support widely employed concepts and practices in feline behavioural medicine. First, classification of cats' problem behaviours relies heavily on approaches derived from studies of their behavioural ecology and, to some extent, extrapolation from canine studies. Few studies have focused on cats in the home, the environment in which most behavioural disorders are expressed. Secondly, cats' chemical senses (olfactory and vomeronasal) are far more sensitive than our own, making it difficult for owners or clinicians to fully comprehend the sensory information upon which they base their behaviour. Thirdly, although the concept of psychological distress is widely invoked as an intervening variable in behavioural disorders, there are still no reliable measures of distress for pet cats in the home.

Global importance: Psychological distress of some kind is the primary cause of many of the behavioural problems presented to clinicians, but surveys indicate that many more cats display the same clinical signs without their owners ever seeking help. The welfare of this 'invisible' group could be improved by veterinarians taking a more proactive approach to educating their clients about the behavioural needs of pet cats.

Feline behaviour: some fundamental misunderstandings

Cats are often portrayed as easier to keep than dogs, providing little incentive for owners to consider how best to provide for their newly acquired pet. Fundamental misunderstandings of feline behaviour and motivation abound. For example, unlike dogs, which use play as a form of social transaction, adult cats' motivations for 'playing' are focused around predatory behaviour, during which they become largely oblivious to their owner's involvement (see box below). Many owners believe that their cat's behaviour is driven by emotions such as jealousy and pride, and cognitive abilities such as deliberate deception, none of which are compatible with biologists' current understanding of the feline brain. A substantial minority believe that their cats are incapable of feeling anxious, the emotional response that is implicated in problematic behaviour more than perhaps any other.⁷ Such misconceptions lead directly to the development of problem behaviours: new owners given basic information on what to expect of their cats, and how to manage their environment, report far fewer problems than owners left to find out for themselves.⁸

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The process of domestication – and its shaping of feline behaviour

The generally accepted framework for understanding the normal behaviour of the household cat is by extrapolation from its wild ancestors and feral counterparts, rather than direct observation of behaviour in the home (in stark contrast to human psychology, in which the evolutionary approach is a relatively new player and still pretty controversial). Our understanding of the derivation of the domestic cat from its ancestral species, the African/Arabian wildcat *Felis silvestris lybica*, has been revolutionised by recent analyses of the DNA of both living cats and museum

specimens from around the world,⁹ doubling the archaeologists' estimate of the time since domestication began, from 5000 to 10,000 years ago, towards the end of the Neolithic period.

The first phase, for which it must be said there is little supporting archaeological evidence, appears to have been essentially evolutionary, as a small number of wildcats found themselves capable of adapting to the new niche created by the concentrations of rodent prey around the poorly protected food stores of our hunter-gatherer ancestors. With the advent of cereal-growing, this niche would have become yet more profitable, permitting a genetic separation between those wildcats that occasionally raided farmsteads but otherwise retained their normal hunting behaviour, and those few cats that happened to have the right temperament to live permanently within human settlements, thereby generating the new subspecies *Felis silvestris catus* that eventually became the pet cat of today. Tolerance of humans would have been essential to allow these cats to exploit both the prey and the shelter (crucially, denning sites) available within these early villages. At some point within the first 1000 years or so of this developing relationship, our ancestors began to transport cats from place to place, as shown by the appearance of cats on Cyprus (which has no native wildcat) about 9000 years ago.

To begin with, these cats would probably have been almost as solitary and territorial as their wild counterparts, a tendency that persists, albeit in a diluted form, in our pet cats. However, with the emergence of the first towns, the quantity of vermin available in a small area would have increased to more than could feed a pair of cats and their offspring, and tolerance of the proximity of other cats would have become an important adaptation, gradually evolving into the cooperative social behaviour seen in today's farm cat colonies.¹⁰

Behaviour we label as 'play'

In cats, the behaviour that we label as 'play' is invariably focused on some kind of object, whether that be a commercially produced toy, a leaf blowing in the wind, or (less advisably) the owner's fingers or toes. In contrast to dogs, where many of these 'games' have a social purpose,³ the way in which cats play with objects is precisely what would be predicted if those objects were potential items of prey.^{4,5} Fur- or feather-covered exteriors are preferred over other textures, as are toys with 'legs', and also toys that disintegrate during play, convincing the cat that it is making progress towards a 'kill'.^{4,5}

Apparently spontaneous movements of the object activate and intensify play, irrespective of whether there is a human agent involved. The movements of the cat's limbs and jaws precisely mimic those made towards prey that is the same size and shape as the

'toy': cats play with mouse-sized toys as if they were mice, rat-sized toys as if they were rats. Hunger causes play to become more intense,^{4,5} and emboldens cats to interact with large toys that they would normally be wary of, in just the same way that a hungry cat will double its efforts to achieve a kill. If play was a purely social activity, it should be suppressed, not activated, by hunger.

This is not to say that cats do not enjoy playing with toys. Each segment of the predatory sequence, from stalking through to close-quarters interaction with the prey, is rewarding in itself, whether or not the cat's efforts eventually result in consumption of food. For cats that readily engage in play, brief 'games' can be used as positive reinforcement, providing a useful alternative to food and petting when training them.⁶

Cats may look like they are playing, but in their heads they are hunting.

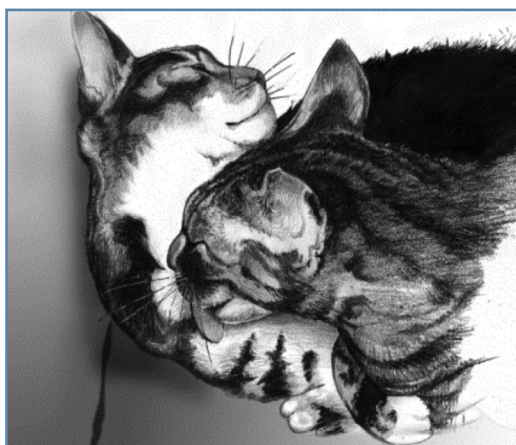


Figure 1 Mutual grooming appears to reinforce bonds within existing social groups. From 'Cat Sense',¹¹ used with permission of the artist, Alan Peters

The social organisation of the cat colonies that form around abundant food sources has proved of considerable interest to biologists, because so few other species in the cat family live in permanent groups, the prime exceptions being the lion and the cheetah. Unlike both of these, males of the domestic cat do not cooperate with one another; it is the females that form the nucleus of social groups, in which related individuals assist one another in the raising of kittens. The behaviours that knit these groups together – mutual flank-rubbing and grooming (Figure 1) – have obvious parallels in the way that many pet cats behave towards their owners,¹⁰ including rubbing around their legs and attempting to lick their hands, for example.

The second phase, domestication proper, began in Egypt about 5000 years ago, which is where we have the first archaeological evidence for cats as pets. It is unclear whether and to what extent this marked another change in the cat's behavioural genetics, this time towards people, or a cultural shift in how cats were perceived – pet dogs, the obvious precedent, had already been popular for many centuries. Subsequently, cats achieved considerable religious significance in Egypt, before being transported all over the known world during the Classical period, beginning around 2500 years ago. The first cats to arrive in Britain were probably brought there by Phoenician traders, about 300 BCE. For the next 1000 years or so most cats would have been pets second and mousers first. Unlike dogs, which would have been most helpful when trained to perform whatever tasks were required of them, cats control vermin most effectively when left to their own devices, counteracting any tendency for cats to become ever more sociable as they adapted to living at increasingly higher densities.

During the Graeco-Roman period, domestic cats were transported both east and west, into areas where they came into contact with and could interbreed with native wildcats of

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different subspecies, *Felis silvestris silvestris* in Europe and the desert wildcat *Felis silvestris ornata* in what is now Pakistan and western India. The DNA of today's pet cats shows little if any trace of either,⁹ although there were descendants of Indian desert cats living in Turkey in the seventh century,¹² and it is conceivable that some of their descendants remain as part of the local pet population, even today. The slender oriental body plan that subsequently gave rise to the Siamese and similar breeds evolved in genetic isolation¹³ (wild *Felis silvestris* does not occur in the Far East) and is an adaptation to humid environments; its DNA does not point to descent from the superficially similar desert wildcat, as was once thought.

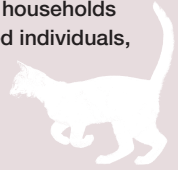
In Europe, the second millennium witnessed intermittent persecution of cats and their owners, slowing the process of domestication; pet cats remained a rarity, perpetuating genotypes that maintained wild-type hunting and reproductive behaviour. As a consequence, the behavioural differences between today's pet cats and their wild ancestors may be traceable to changes in as few as a dozen genes.¹⁴ It was not until the 19th century that keeping a cat primarily for its company became at all widespread in Western Europe or the United States, and the trend towards cats becoming the most popular pet in both regions only took off a few decades ago.

A second factor that undoubtedly slowed domestication is the cat's hypercarnivory. All felids require a flesh-based diet, due to a set of ancient mutations that restricted their ability to process plant-derived foods. In addition to their need for relatively large amounts of sulfur-containing amino acids (methionine, cysteine, taurine) and the vitamins niacin and thiamine in their diet, they also require essential fatty acids of animal origin in order to synthesise prostaglandins, which most other mammals can make from plant-derived precursors. Cats also need a constant supply of high quality protein, as they are unable to switch off amino acid catabolism, again tying them to their carnivorous lifestyle. In this sense they are quite unlike dogs, which can switch to plant-based foods when meat is scarce. The cat's basic nutritional requirements were not properly understood until the 1970s, so it has only been since then that cats have been able to reproduce successfully without supplementing their diet through hunting. This provides one explanation for their persistent habit of patrolling and attempting to defend a hunting territory, even when well fed by their owners: too few generations have passed since this has no longer been a necessity for their fundamental motivations to have changed appreciably (although in theory these might be reduced in the future by directed breeding).¹⁵

Biological factors influencing problem behaviours in cats

- ❖ Unlike dogs, derived from the highly social wolf, domestic cats are descended from a solitary territorial ancestor.
- ❖ Until the latter half of the 20th century, cats were mainly valued for their abilities as independent hunters, for which a social bond with humans or other cats was unnecessary.
- ❖ Cats have specialist nutritional requirements that impeded their becoming wholly dependent on their owners.
- ❖ Cats prioritise territory over social interaction with their owners, the opposite to dogs.

- ❖ During their domestication, cats evolved a simple, female-based, social system, but their default is still to be antagonistic towards unfamiliar cats (dogs have lost the wolf's natural aggression towards members of other packs). Multi-cat households are usually artificial assemblages of unrelated individuals, and therefore chronic antagonism is likely between at least some pairs of individuals.
- Cats residing in adjacent households are unlikely to interact amicably.



Cats' sexual behaviour is also largely unchanged from that of their wild ancestors. Pedigree cats being still in the minority, the majority of pet cats are the offspring of unplanned matings that occur when a female comes into season, attracts one or more entire males and engages in wild-type courtship behaviour that originally evolved to ensure maximum fitness for her offspring. (Nowadays in the West, the critical factor determining a cat's lifetime reproductive success, both male and female, must be to escape being neutered,¹⁵ but the full effects of this change, which should lead to those cats that are most difficult to socialise producing the most offspring, have not yet permeated through to the behaviour of the typical cat.)

By comparison with dogs and other common domestic mammals, cats are not yet fully domesticated. They select their own mates, and retain much of the predatory drive of their wild ancestors, both of which require interventions from their owners to counteract their effects. There is an increasing trend, especially in urban areas of the United States and in continental Europe, to keep cats indoors throughout their lives, denying them the opportunity to mate, presuming they are not neutered, and also to hunt wildlife, in addition to protecting them from hazards such as diseases and road traffic. The cost of such confinement to their mental wellbeing has been much debated but inadequately quantified.^{16,17} In the UK, cats allowed outdoors are frequently neutered¹⁸ and may be fitted with a bell or other deterrent device to reduce their impact on bird and small mammal populations, although the most effective suppressor of 'serious' hunting behaviour is probably a nutritionally complete diet,¹⁹ such as most pet cats in the West receive.

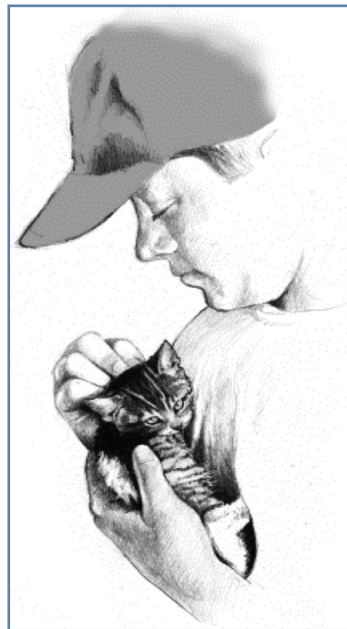


Figure 2 Gentle handling promotes socialisation in kittens of all ages. From 'Cat Sense',¹¹ used with permission of the artist, Alan Peters

Cats as individuals – learning and 'personality'

Although cats are generally (though wrongly) perceived as being less trainable than dogs, learning plays a major part in the way both species behave. Thus how a given cat reacts to a particular situation will vary considerably depending on its lifetime experience; albeit genetic variation between individuals does also play a part, if only in channelling learning in different directions. The environment that cats find themselves in, and its match with their formative experiences, also appears to play a critical role.²⁰

The most important determinant of how a cat reacts to humans is its experiences during the socialisation period, which in this species runs from 2–9 weeks of age, earlier than in the dog. Kittens that have not been handled by the age of 9 weeks do not approach people spontaneously, and usually become 'feral', the most likely scenario being that their mother was also feral and therefore chose to give birth and nurse her kittens in some out-of-the-way location. This is not to say that 9-week-old kittens have learned everything about people that they ever will; rather, handling during the socialisation period opens a window that enables continued positive interaction with humans and promotes learning of how to interact with them (Figure 2). This process seems to be particularly formative during the next 4 months or so, such that for most cats the style in which they interact with people becomes fixed by the time they are about a year old.^{21,22}

The corresponding optimum period for learning how to interact with other cats has not been studied systematically, which is unfortunate, since incompatibilities between cats in the same or neighbouring houses cause a significant proportion of problem behaviours. Hand-raised kittens that do not receive any contact with other cats during the socialisation (to humans) period are anecdotally considered to be at enhanced risk of developing problems such as



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nervousness, aggression and a reduced ability to cope with changes in their environment. Others may become overattached to their raisers or subsequent owners, attempting to suckle from fingers or elbows even when adult.

The vast majority of cats that are presented at clinics for behavioural problems are neither feral nor hand-raised, but nonetheless display considerable variation in 'personality' from one individual to another. Pedigree cats as a whole do appear to be more likely to be presented with problem behaviours. However, this may be due as much to owner expectations and emotional and financial investment as to differences in the cats' experiences – ordinary domestic cats or 'moggies' are typically raised informally in family surroundings and rehomed at 8 weeks, whereas pedigree cats are often bred in purpose-built housing and are normally homed at 12–16 weeks of age, potentially restricting their socialisation. There are undoubtedly genetically based differences in temperament between breeds,²³ but there is little hard data on how these translate into the prevalence of behavioural disorders.

Non-pedigree pet cats also vary in temperament and therefore in their susceptibility to different problems. Early attempts to classify the main personality types suggested that there are three broad categories: cats that are confident and inquisitive, cats that appear timid and nervous, and cats of both kinds that are more or less active than the norm. The bold/shy axis, which has also been detected in many other species, can have a genetic basis in cats, although some elements are undoubtedly learned.²⁴ Problematic behaviour is presumably affected by many genes; one of these, coding for an oxytocin receptor, has been recently identified as contributing to irritability.²⁵ More such identifications will doubtless follow, offering the possibility that genetic typing may eventually become a tool in the veterinary behaviourist's armoury.

Although the assessment of temperament differences between cats has recently received attention from scientists,²⁶ this has mostly been based on owners' subjective perceptions of their cats, rather than measuring their behaviour directly:^{27,28} this method interposes an unhelpful curtain of anthropomorphism between the data gathered and genuine and reproducible characteristics of the cats themselves. A more objectively based tool – the Feline Behavioural Assessment & Research Questionnaire (Fe-BARQ) – has recently been validated, and has demonstrated the complexity of cat-to-cat variation in behaviour, identifying no fewer than 17 underlying types of variation, including playfulness, sociability to people, attention-seeking and fear of other cats.²⁹ It may eventually provide clinicians with a useful starting point for assessment of their patients' basic 'personalities'.

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The subjective world of the cat – senses

Cats being mammals, it is easy for owners to presume that the world that they themselves perceive is identical to their cat's. The biological reality is that subjective impressions of their surroundings differ between our two species at three levels: the information gathered by the sense organs, the manner in which this information is integrated and filtered by the brain, and the emotional reactions that are triggered. Were more owners to fully comprehend these differences, and react appropriately, many problem behaviours might not escalate to the point of requiring veterinary intervention.

Cats' sense of hearing and vision are both different to our own, even though the corresponding sense organs are constructed along the same mammalian pattern.³⁰ The range of frequencies that cats can detect encompasses all of those that we can hear, except for very low-pitched notes, which cats can probably detect using the sensitive pads on their toes. Cats can also hear more than an octave above our own range, into the 'ultrasound' region: this is an adaptation that enables cats to eavesdrop on the ultrasonic calls that small rodents use for communication. In terms of the physics of how the mammalian ear works, this ability is unremarkable, as the hearing range of the ear should go up as it gets smaller. What is actually unexpected is the cat's ability to hear low-pitched sounds, including men's voices. This has been traced to a septum that alters the resonant properties of the middle ear, which is also found in other species of small cat, so did not evolve during domestication; rather, it was a lucky accident that enabled even the earliest domestic cats to detect and react to male voices.

The cat's eyes are adapted to provide accurate vision in very low light. They are large by comparison with our own, with even larger pupils, both factors maximising the amount of light entering the eye. The reflective tapetum behind the retina further increases the efficiency of the eye (and also gives the cat the eye-shine that inspired the eponymous road-markings). Most of the detectors on the retina are rods, with relatively few of the cones that give us our daytime colour vision; cats are not only red-green colour blind, but when their brain interprets the information coming from the retina, it prioritises outline, brightness and especially movement over colour, almost the exact opposite to ourselves.

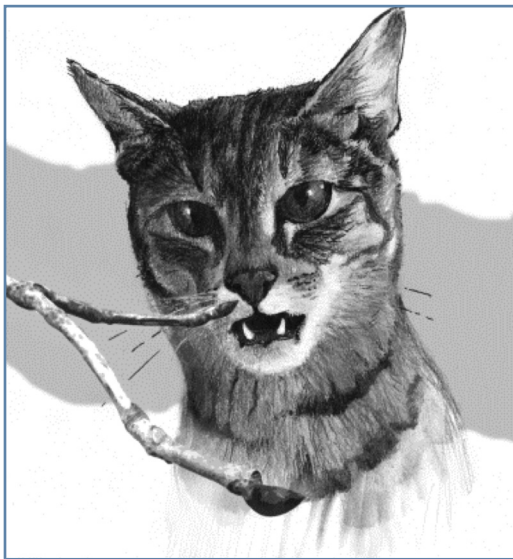


Figure 3 Flehmen. From 'Cat Sense',¹¹ used with permission of the artist, Alan Peters

Hearing and vision are sufficiently similar between cats and their owners that there are at least common reference points: this is not true of olfaction. Akin to most mammals, with the exception of higher primates like ourselves, cats rely on odour both to communicate with one another and to gather information about many aspects of their environment. Not only are their noses about a thousand times more sensitive than ours, cats possess a second olfactory detection system, the vomeronasal organ. Lying between the hard palate and the nostrils, this acts as a kind of half-way house between smell and taste, mainly detecting chemicals that have dissolved in saliva as the cat opens its mouth in the characteristic grimace known as 'gaping' or 'Flehmen' (Figure 3). Reliance on these chemical senses is so removed from our own experience that it is difficult enough for biologists and veterinarians, never mind owners, to imagine what the world must be like for an animal that is far less visually obsessed than we are. It is therefore unsurprising that what we presume (unable to experience them for ourselves) are disturbances of the olfactory environment make a significant contribution to so many problem behaviours of cats.

Although there has been very little research into how cats interpret the odours they encounter, the importance they place on them is indicated by the effectiveness of behaviour modifications using odour cues. Thus, for example, a cat that has lost its characteristic odour due to a period of hospitalisation may be attacked by other cats in the household when it returns. Anecdotally, the process of introducing two previously unacquainted cats to one another can be smoothed by allowing

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each several experiences of odour collected from the other, well before any face-to-face encounter.⁶ Seemingly, what each animal learns from this process is that the cat bearing the unfamiliar odour is in the vicinity (how else would its smell have got there?) but has not presented any threat. When the other cat is eventually introduced, the resident cat will be able recognise it by its odour (and vice versa) and both will be less likely to default to defensive mode. Other pre-exposures to unfamiliar scents in neutral or deliberately rewarded contexts presumably work through a combination of habituation and positive association: examples include habituation to the odour of items brought into the house in preparation for a new baby. Olfactory enrichment is effective for cats in rehoming centres,³¹ and therefore probably for pet cats also.

Although domestic cats routinely deposit scent marks on objects in their environment, remarkably little is known about their function.³² The external ears, the temples, the cheeks and the corners of the mouth all produce scents, some or all of which must be deposited when a cat cheek-rubs an object or another cat, and there is also a gland beneath the chin that is discharged during chin-rubbing behaviour (Figure 4). Scent-producing glands are additionally found between the toes, which presumably leave scent behind whenever the cat scratches with its claws. There is another cluster of odour-producing structures at the rear end, including the preputial and anal glands, the scent from which can be dispersed by urination and defecation, respectively, as well as skin glands in front of and down the length of the tail.

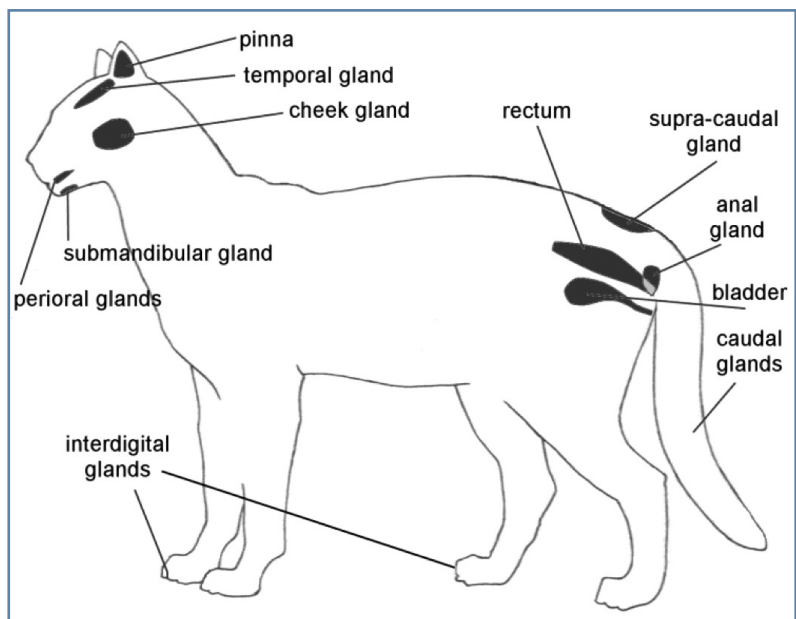


Figure 4 Main scent-producing structures of the domestic cat

Cats' brains have relatively large areas devoted to olfaction, and also balance, as befits their lifestyle.



It is claimed – though the primary data appears only in a patent application – that the various facial glands of domestic cats produce several chemical compounds (or mixtures) that have distinct behavioural effects.^{33,34} One named F3 is widely used in behaviour modification in its commercial form (Feliway; Ceva). It is stated that this mimics a chemical signal that cats deposit around their familiar home ranges and ‘helps in organising the environment by classifying it into known objects and unknown objects’.^{33,34}

From an adaptationist perspective this seems an unlikely hypothesis. Mammalian chemical signals are formally divided into two types: pheromones, which have a communicative function common to all individuals within a species, and ‘signature mixtures’ that identify each individual to others (and quite possibly to the individual that deposited the scent upon returning later to the same site).^{35,36} Pheromones are deployed in situations where it is advantageous to both the emitter and the receiver that some simple message is understood, and so vary little between individuals; the odour given off by a female in season is a case in point (note F3 is marketed as a ‘pheromone’). Signature mixtures vary from one individual to another and have to be learned by recipients. The anal gland secretions of cats fall into the category of signature mixtures,³⁷ differing reproducibly from one cat to another, and it seems likely that this is also true of the cheek gland secretions.

Since it is implausible that any artificial odour could match that of the cat in whose house it was being dispersed, the cat should logically interpret the synthetic odour as belonging to some other cat that has invisibly scent-marked its territory. Lack of clarity as to the mode of action of Feliway may explain why different investigators have found very different levels of efficacy.^{38,39}



It is difficult to explain cat behaviour without invoking the triggering of simpler emotional states, such as anger, affection, fear and anxiety.

The subjective world of the cat – cognition and emotion

Great strides have been made over the past two decades in understanding the cognitive abilities of dogs; in addition to testing their behaviour, it has proved possible to train dogs to undergo fMRI (functional magnetic resonance imaging), which has revealed, for example, signs of emotional responses specific to images of the dog’s owner. Cats, though equally trainable,⁶ lag far behind in corresponding research.²⁶ However, it has been possible to show that cats do form genuine attachment bonds with their owners, and modify their behaviour accordingly.^{21,22} Thus, despite the scepticism of some, there is a logical basis for separation disorders in (perhaps a small minority of) cats.

Some inferences can be made about feline cognition based upon what we now know about dogs, since their brains are both constructed according to the carnivore pattern, and are therefore substantially different to our own. Relative to the size of their bodies, cats’ brains are less than half the size of ours, and much of the difference is due to our comparatively huge cerebral cortex, the ‘thinking’ part of our brains. Cats’ brains have relatively large areas devoted to olfaction, and also to balance (the cerebellum), as befits their lifestyle. In terms of behaviour, the structure of their brains suggests that cats almost certainly live much more in the present than we do, neither ruminating on the past nor planning for the future.

These cognitive differences also have consequences for cats’ emotional repertoires. Contrary to what many owners believe, cats are probably incapable of experiencing emotions such as guilt, pride and grief, all of which require a sense of self and/or a concept of past, present and future. (Cats do appear to grieve for missing feline or human companions, but this behaviour can be neatly explained by the lingering odour of the absentee, undetectable to us but all too real to the cat.) Simpler emotions, what we might refer to as ‘gut feelings’, such as anger, affection, fear and anxiety, are generated in the limbic system, which is common to all mammals. Due to the differences between their brains and ours, cats may not experience these quite in the way we do, but it is difficult to explain cat behaviour without invoking the triggering of these simpler emotional states.

Behavioural disorders – why ‘problem’ or unwanted behaviour develops

A change in their cat’s behaviour is often what prompts owners to consult a veterinarian, whether the cause of that change is ultimately psychological (a ‘problem behaviour’) or physiological (eg, a pathology or a hormonal disorder). It is conventional to divide behavioural problems of cats into those that are essentially adaptive responses insofar as the cat is concerned, but inconvenient or distressing for the owner, and those that have medical causes, such as epilepsy or hyperthyroidism; although, as has been pointed out,⁴⁰ in real life many cases comprise elements of both, and variable combinations of adverse early life experiences and psychological stress can lead to or exacerbate medical conditions, such as chronic lower urinary tract signs.⁴¹ The focus of the remainder of this discussion is exclusively behaviour that can be interpreted as a normal adaptive response to the situation the cat finds itself in.

Owners’ lack of understanding of normal cat behaviour can lead to errors in management which, in turn, impact negatively on welfare. To take one common example, house-soiling; many owners do not appreciate that cats that use indoor litter trays rely on cues such as location, odour and texture of the substrate when choosing where to eliminate. The cat may not ‘know’ that the litter box is the place that the owner wants them to urinate and defecate, but some owners evidently believe the opposite, attributing motivations

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such as ‘spite’ to the cat when a change in its environment causes it to urinate elsewhere in the house. Under these circumstances, punishing the cat for its supposed transgression is likely to lead to a vicious spiral in which the anxiety that caused the original incident becomes magnified at every recurrence. Resolution of house-soiling requires comprehension of the cat’s perspectives, including a location that smells very slightly of urine and faeces (to the cat’s nose, and probably unnoticeable to the owner), thus indicating a location that has been used previously; but equally, not strongly, which might otherwise indicate an area that has been over-used and would in the wild present a risk of infection by parasites.⁴² In multi-cat households, individual cats that tend to avoid one another will be especially wary while urinating and defecating, but very often such cats will not have been provided with multiple litter trays.

As a second example, many owners are annoyed by their cat’s instinctive habit of scratching on friable surfaces, behaviour that is perfectly natural from the cat’s perspective, and only a problem to the owner. Scratching can be redirected away from furniture and curtains using standard training techniques, yet declawing (onychectomy) is still widely used, where legal, as a less labour-intensive option. However, in multi-cat households declawing doubles the risk of house-soiling, possibly because these cats are less able to defend themselves against other cats, so potentially replacing one problem with another while at the same time threatening the cat’s welfare.^{43,44}

Owner psychology vs cat welfare: a mismatch

There appears to be a considerable mismatch between the occurrence of potentially problematic behaviour in the pet cat population, and its prevalence in terms of numbers of enquiries to advice services and cases presented to practitioners (Figure 5). Behaviour that causes inconvenience or embarrassment to owners, especially urination and defecation in undesired locations, is over-represented in clinical surveys; behaviour that may be perceived as ‘just what cats do’, such as aggression between cats living in neighbouring households, is under-represented, even though these may be different expressions of the same underlying issue. In one door-to-door survey, over half of all owners reported that their cat was fearful of unfamiliar people and/or neighbourhood cats,⁴⁵ yet it seems that few owners perceive such behaviour as a problem worth addressing, regardless of its effect on their cat. Thus although owners, and especially those who seek professional help, are likely to have

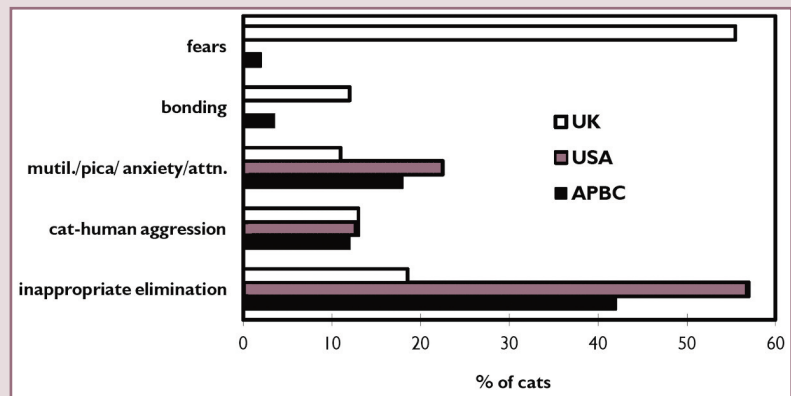


Figure 5 Percentages of pet cats reported to display problematic behaviour. Data were gathered from a door-to-door survey of owners (UK), spontaneous enquiries to an ‘ask the cat expert’ website advertised on the Discovery Channel (USA), and referrals of cats to the UK-based Association of Pet Behaviour Counsellors (APBC). Mutil./pica/ anxiety/ attn. = total for self-mutilation, pica, separation anxiety and attention-seeking⁴⁵

their cat’s best interests at heart, their conception of what constitutes good welfare in their pet may be significantly skewed.⁴⁶

Most behavioural disorders seem to result from the cat being prevented from achieving emotional equilibrium, either due to a perceived or actual external threat, or frustration at being prevented from performing its natural behaviour. Such cats are conceived of as experiencing distress,⁴⁷ which then leads to changes in behaviour such as enhanced aggression or flight behaviour, or attempts to manipulate the olfactory environment by changing the location of scent-marking, including urination and defecation. Cats may perceive threat when their access to an adequate home range is or becomes restricted, including being kept indoors,⁴⁸ changes in household routine, or evidence that other cats or other animals are intruding into the cat's core areas: changes in odour profile must play a large, possibly predominant role in all of these scenarios. More direct social stressors include physical conflict with other cats, both within and outside the owner's house, and with humans. The latter may be due to the cat having adopted inadequate or malfunctioning strategies for reacting to certain people or, indeed, all humans, usually a consequence of inadequate socialisation, or having received aversive experiences at the hands of its owners, such as physical punishment.⁴⁷

While perceived threat may be conceptually useful in diagnosing unwanted behaviour, it has not proved straightforward to derive reliable independent measures of distress in pet cats. For example, the stress hypothesis predicts that multi-cat households should contain a higher proportion of stressed individuals than among single cats; however, three recent independent studies have been unable to confirm this.^{49–51} The Cat-Stress-Score, a composite behavioural measure validated for use on caged cats, is not easy to apply in domestic situations.⁴⁹ Physiological methods might be more useful for clinicians, but cortisol, the hormone that is widely used to assess chronic stress in other species, seems to be difficult to interpret in cats, whether measured in faeces or in urine. Chronic distress can induce a range of non-specific signs, including vomiting, diarrhoea, anorexia, fever, lethargy, feigned sleep and inhibition of grooming or overgrooming.²⁰



Most behavioural disorders seem to result from the cat being prevented from achieving emotional equilibrium, either due to a perceived or actual external threat, or frustration at being prevented from performing its natural behaviour.

KEY POINTS

- ❖ The conceptual basis for the classification of cats' behavioural (non-medical) disorders is much less secure than a quarter-century of generally concordant literature might suggest.
- ❖ There has been very little research into the behaviour of cats in 'normal' households (ie, those that do not seek advice from clinicians), but it seems likely that in many of these the owners are simply tolerant of behaviour that others consider problematic. The population of owners, and thus cats, seen by clinicians may therefore select itself more on the basis of owner psychology than cat welfare.
- ❖ The widespread assumption that many disorders are due to general psychological distress has not been proven. Explanations will have to be found as to why some cats respond in one way, others in another; why some cats seem to have their own ways of coping, at least to their owners' satisfaction, while others do not.



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Dedication

This review is dedicated to the memory of Sir Patrick Bateson, who did so much to promote the study of the behaviour of domestic cats as a legitimate branch of ethology.

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