

Conspecific and Human Sociality in the Domestic Cat

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Contributor: lauren finka

Sociality can be broadly defined as the ability and tendency of individuals to reside in social groups with either conspecifics and/or other species. The domestic cat is the only species within the *Felis* genus to have transitioned from a wild, solitary species to one of the most popular human-companion animals globally. In stark contrast to their closest wild ancestors, the domestic cat displays an impressive capacity to cohabit successfully with both humans and other cats. However, at an individual level, domestic cats demonstrate substantial variability in their sociability towards both species. Such variability may be influenced by a range of factors including their early life experiences, genetic selection, and individual cat and human characteristics, in addition to various factors associated with their social and physical environment. The impact of these factors may have important implications regarding a cat's social relationships, their adaptability to various social contexts, and, ultimately, their wellbeing. In line with modern pet-keeping practices, domestic cats may often be exposed to lifestyles which present a range of complex social and environmental challenges, although it is unclear how much cats have been selected by humans for traits that support adaptability to such lifestyles.

Keywords: sociability ; wellbeing ; stress ; group living ; domestication ; felis

1. Introduction

In a relatively brief period of evolutionary time, the domestic cat has transitioned from a wild solitary species to one of the most popular companion animals globally. During their initial domestication (from wild populations of *F. silvestris lybica* ^[1]), natural selection pressures are likely to have favoured bolder individuals, as well those with a greater tolerance to human and conspecific proximity ^[2]. Subsequently, as the value of cats as a source of human companionship increased, a degree of active selection by humans for cat tractability likely followed ^[3]. However, even within modern-day domestic cat populations, it is unclear of the strength to which (both human and conspecific) sociality has been selected (either naturally or artificially), given that (i) domestic cats may still be motivated to seek out a primarily solitary existence, and can survive under such conditions ^{[4][5][6][7]}, that (ii) socialised cats from companion populations may live and/or readily interbreed with unsocialised cats from free-living populations, and additionally that (iii) the most intensive period of humans' cat selection has occurred within the last century, with aesthetic features largely prioritised over traits that might enhance sociability towards conspecifics and/or humans ^{[1][8][9]}.

Despite these possible constraints to cats' sociality, the domestic cat is still capable of residing within social groups and may actively choose to associate with conspecifics and/or humans, in each case potentially developing positive social relationships. In both free-living populations, as well as those managed by humans in confined environments, cats may display a range of affiliative behaviours. Affiliative behaviours directed towards conspecifics include vertical tail raising on approach (e.g., the 'tail up' signal), as well as initiating various forms of physical contact including nose touching, play, allo-grooming, allo-rubbing, tail wrapping, and sleeping and resting together or in close proximity ^{[10][11][12]}. Vocalisations such as purring and meowing between mother and offspring dyads occur frequently and are thought to serve important communicative and care solicitation functions ^{[13][14]}. Similar social behaviours are often directed towards humans during cat-human interactions ^{[15][16][17][18][19]} and cats are well documented as having the capacity to develop affiliate social relationships with people ^{[20][21][22][23]}.

At a species level, the domestic cat occupies a diverse range of lifestyles with varying degrees of association with conspecifics and humans ^[24]. Broad lifestyle categories include cats that can be described as free-living (i.e., feral, street, or stray cats) and those that are living in confined environments managed by humans (e.g., the domestic home, shelter or rehoming centre, and research facility). In many cases, close associations with conspecifics and/or humans may promote health advantages for cats. For individuals under some form of human management, these typically include the provision of primary or supplemental feeding, veterinary care, and access to warm, sheltered, and safe environments. For cats outside of human management, the benefits of living with conspecifics may include communal raising of offspring and shared access to clumped resources of value such as food and shelter.

At the same time, cats are considered to be 'socially flexible' rather than 'socially obligate', meaning they possess the potential to adapt to different forms of social living, but that group living (with conspecifics and/or humans) is not necessary for their survival. Degrees of sociability may be highly variable at the individual level, even amongst those occupying similar lifestyles ^{[22][25]}. Within lifestyle categories, the availability and quality (i.e., distribution and abundance) of the cats' physical resources can vary greatly ^{[26][27][28]}, as can the characteristics (e.g., age and sex, personality, previous experiences) of the cats and/or humans with which individuals cohabit ^{[29][30]}.

Variability in cats' social behaviour towards both humans and conspecifics, as well as the impacts of cohabitation on their wellbeing, may be influenced by a range of ontogenetic ^[31] and genetic factors ^[32] and their potential interaction ^[33] in addition to the various social and environmental parameters associated with their specific lifestyle ^{[12][34][35][36][37][38]}. Thus, in certain instances, close associations with humans and/or conspecifics may be detrimental rather than beneficial to the cats' wellbeing, especially where individual social flexibility or adaptability is limited ^{[39][40]}.

2. Proximate Factors and Their Links to Conspecific Social Behaviour in Free-Living Populations

In free-living populations, cat density and active group living is primarily determined by resource abundance and distribution, with cat densities increasing, and groups typically forming, where resources are plentiful and localised (e.g., refuse areas, farm buildings, or supplemental feeding stations) ^{[26][29][41]}. The nature of group-living and conspecific social interactions may be influenced by a range of factors such as relatedness and familiarity, age, sex and sex ratio, and individual personality, in addition to human intervention (e.g., resource provisions and neutering). Where group living occurs, these may often be matrilineal in structure, being comprised of related females, their offspring, and immigrant adult males ^{[29][41][42]}. Agonistic interactions amongst free-living individuals are described as rare, but occurring more frequently towards unfamiliar/unrelated cats (i.e., non-group members), particularly those that are female ^{[41][43]}. Amongst group-living adults, individuals are also described as having 'preferred associates' with which they spend proportionality more time in proximity to and perform affiliative behaviours towards ^{[11][29][41][44]}. Amongst offspring, observations of related juveniles and kittens suggest individuals prefer to associate with conspecifics of a similar age category to themselves and littermates over non-littermates ^[29].

Rates of agonistic behaviour between group members have been explained as a function of variation in age and sex ratios in males, and of neuter status in both males and females. For example, in a (presumably intact) colony with larger male to female and adult-male to juvenile-male ratios, adult males were reported to initiate aggressive behaviour towards other adult males more often than other sex-age classes ^[29]. In contrast, in a colony where adult male to female and adult-male to juvenile-male classes were smaller, adult males were observed to initiate aggressive behaviour most frequently towards juvenile males ^[29].

Amongst free-living cats, personality differences may also influence the general behavioural styles of individuals towards conspecifics, although there is limited research within this area. In a study of unneutered male cats across several colonies ^[45], cats were described as having either predominantly 'proactive' or 'reactive' personalities. 'Proactive' males were defined as those engaging in more agonistic (e.g., threatening, fighting, and chasing), but also affiliative (e.g., 'nose sniffing, passive contact, and rubbing'), interactions with other group members. In contrast, 'reactive' individuals were mostly characterised by displaying avoidant (e.g., 'avoiding, crouching, flying, hissing') and less agonistic behaviour.

3. Proximate Factors and Their Links to Conspecific Social Behaviour in Confined Populations

For cat populations managed in confined environments, group-living and group composition are primarily dictated by humans, and, thus, cats have little choice over this aspect of their sociality. Despite this, cats may still display individual variation in the conspecifics they choose to associate with or avoid ^{[46][47]}. Variations in the nature of conspecific social interactions have been linked to similar factors to those highlighted in free-living populations, although these relationships and their direction of effects are not consistent across studies. For example, in a USA-based survey of cat owners that had recently introduced a cat into their household ^[48], the provision of outdoor access (but not cat age, sex, or cat group size) was associated with increased rates of fighting amongst cats. In contrast, a more recent (USA) study ^[12] based on a substantially larger population of cats and owners reported that age (i.e., younger cats), sex (i.e., female), multi-cat group size (i.e., larger), as well as the recent addition of an unfamiliar cat to the home, were all associated with increased rates of cat conflict, whilst the provision of outdoor access was not.

Initial behavioural responses during introductions are considered important determinants of the future relationships between cohabiting cats. For example, the same study ^[12] reported greater rates of conflict and lower rates of affiliative behaviours between cats in households where owners indicated initial introductions 'did not go well', with similar results reported in ^[48]. In general, gradual methods of cat introductions are considered to help promote more amicable conspecific relationships. Such methods incorporate scent swapping between cats before progression to (slowly increased) periods of visual, and then supervised, physical access. However, while these methods are widely recommended ^{[49][50][51]}, their benefits are currently based on anecdotal observations rather than empirical research. In the one study where current rates of fighting were assessed relative to methods of cats' initial introductions (i.e., either 'gradual' or 'immediate') ^[48], no significant differences were reported between owners using either method. However, the author highlighted issues associated with the way that 'gradual' and 'immediate' methods were categorised, potentially resulting in less than meaningful statistical comparisons. For example, 'gradual' introductions encompassed a broad range of time periods, from hours to weeks, and did not include any details of the specific methods used (e.g., scent swapping or visual access initially). Further study into the potential benefits of gradual approaches during cat introductions and their impact on long-term relationships are therefore warranted.

Familiarity, relatedness, and social exposure during the sensitive period (i.e., approximately between 2–7 weeks of age) have also been linked to differences in conspecific social behaviour. In observations of mostly unrelated cat dyads within the domestic home, longer lengths of cohabitation were found to negatively correlate with rates of conspecific aggression ^[52]. In observations of cat dyads housed together in a cattery ^[10], litter mates (i.e., related and together since birth) spent more time in physical contact with each other and were more likely to feed together and allo-groom, compared to unrelated pairs (that had previously lived together in a home for at least a year). Rather than simply their genetic relatedness, the authors attributed these greater rates of affiliative behaviours to littermates having been socialised to each other during their sensitive periods and then also experiencing an extended duration of cohabitation due to their remaining together into adulthood. In a large group of confined cats residing in a private property, duration of cohabitation was similarly positively associated with proximity and allo-grooming between conspecifics ^[53].

Within the domestic home, rates of agonistic behaviour have been linked with aspects of cat's personality. In ^[54] a (weak) positive relationship between owner ratings of their cat's level of fearfulness and conspecific aggression (e.g., growls, hisses, bites, scratches) was reported. In ^[12] a (weak) positive relationship between cats described as 'sedentary and shy' and rates of conflict behaviours (e.g., 'flee', 'hiss' and 'twitch tail') was also identified.

4. The Impact of Cohabiting with Conspecifics in Confined Environments on Cat Wellbeing

Given the potential links between increased group size and conspecific conflict ^[12], it is logical to assume that living in larger multi-cat groups may be associated with more negative wellbeing outcomes for cats. In the home, for example, greater numbers of cohabiting cats have been significantly linked to greater rates of owner-reported 'behaviour problems' and anxiety ^[55] and increased house soiling ^{[28][56][57][58]}, but also fewer 'behaviour problems' ^[59], lower Cat Stress Scores or CSS (a posture and behaviour based scoring system) ^{[60][61]}, and less negative interactions with humans ^{[62][63][64]}. Additionally, several studies have reported no significant links between cat group size and 'behaviour problems' ^[65], house soiling ^{[62][64]}, obesity ^[64], or physiological stress ^{[30][66]}.

These equivocal findings potentially arise due to several pertinent factors. Issues associated with the variability of study methodologies and limitations in their designs and analytical approaches mean that the relative effects of cat group size may not be clear and/or comparable between studies, making it difficult to reach a consensus ^[38]. Furthermore, the varied, multi-faceted nature of housing and husbandry conditions to which domestic cats are exposed, and subsequently studied under, in addition to the potential diversity of the individual characteristics of the cats within each multi-cat group, means that cat populations may be very demographically diverse. This may occur both across separate study populations, but also within a single comparison group, within a single study ^[38].

5. Proximate Factors and Their Links to Cat–Human Social Interactions in Confined Environments

Several studies have highlighted various human characteristics as important determinants of cats' social behaviour during human-cat interactions (HCI). Observational studies taking place in the domestic home ^{[67][68]} suggested cats demonstrate preferences for social interactions with adults (particularly females) over children. These differences in cats' responses may be explained by variations in humans' interaction styles, given that children (in particular males) may be more likely to approach resting cats, pick them up, and follow retreating cats than adults, behaviours which are likely to be perceived as

threatening by the cat, or to at least induce a degree of discomfort [67][68]. In contrast, adults (in particular women) may be more likely to vocalise to cats and crouch down to their level, postures and behaviors which may be perceived as a less threatening and more encouraging of the cat to engage in social interactions [68]. In [34] observations of HCI with adult owners in the home suggested that cats interacted with owners for longer durations when the interactions were initiated by the cat as opposed to the owner. Additionally, cats were found to be more likely to engage in interactions when initiated by the owner, if owners were generally responsive to the cats' requests for interactions [34].

Regions of the cats' body that are touched by humans may also impact the nature of their behavioural responses. Human stimulation to the cats' caudal region may produce greater rates of human-directed aggression (e.g., hissing, biting, smacking, or scratching) as well as behaviours indicative of discomfort (e.g., flattening the ears, flicking and/or swishing the tail) [69][70]. In contrast, stimulation to cat's temporal regions may lead to greater rates of affiliative behaviours (e.g., closing or half-closing the eyes, "kneading" with paws, purring, rubbing against the human, and dribbling), with stimulation to the perioral regions, flank, stomach, and back producing much greater between-individual variation in responses [69]. Understanding of the impact of human behaviour styles on cat comfort and social behaviour during HCI (incorporating findings from the aforementioned studies) was recently formalised into a set of 'best practice' guidelines for humans [71]. Compared to control HCI, cats were found to exhibit significantly more affiliative and positively valenced behaviour (e.g., tail waving, kneading, sniffing and rubbing, ears forwards), as well as less agonistic behaviours (e.g., hiss/growl, cuff/swipe, bite) and fewer signs of conflict (e.g., tail swishing, ears rotated/flattened, paw lift, rapid groom, head/body shake, freeze/crouch, avoid/move/turn away), when humans followed the guidelines [71].

In addition to general styles of interaction, certain facial and postural cues displayed by humans may promote more positive social responses from cats. For example, companion cats were found to approach unfamiliar humans significantly more often when they performed a 'slow-blink sequence' towards the cat, rather than when they adopted a neutral expression [72]. Cats were also found to spend a longer time in contact with their owners when they displayed a 'happy' rather than an 'angry' posture and facial expression [73].

The personality of owners has also been linked to more general, longer-term aspects of cats' human-directed social behaviour [37], with the direction of results sharing parallels with those identified within the parent-child [74][75] and owner-dog dynamics [76][77]. In addition to owner personality, various characteristics of the cat and their environment may impact on the nature of their social interactions with humans. Cats' individual characteristics (i.e., see further sections) may also affect their perceived value of human-social interaction relative to other non-social stimuli categories such as food and toys.

6. The Impact of Cohabiting with Humans in Confined Environments on Cat Wellbeing

During typical social interactions with humans, a cat's exposure to a single HCI that it finds aversive may induce an acute (and thus potentially short lived) negative experience (see previous section). In contrast, the repeated, frequent exposure to aversive HCIs is much more likely to induce chronic (and thus longer term) negative states within individuals, potentially leading to their compromised wellbeing. While this line of scientific enquiry remains largely uninvestigated, a preliminary study [78] in the domestic home reported that cats that were described by their owners as generally "tolerating" being stroked had higher faecal glucocorticoid metabolite levels, compared to cats that were described as actively "liking" or "disliking" being petted. Such findings highlight the potential impact of a cat's experiences during petting on their physiological stress response, with cats "tolerating" petting potentially at greater risk of increased stress. However, further research, which considers a range of additional (suitable) behavioural and physiological measures, is warranted in order to understand the implications of aversive HCI to cats' wellbeing more broadly.

In [37], cats of more neurotic owners were reported to display greater stress-linked 'sickness behaviours' (a composite score representing poorer coat condition, greater frequencies of cystitis, vomiting, diarrhoea, and constipation). These cats were also more likely to have an existing medical condition, to be of an unhealthy weight, and were more likely to have either restricted or no access to the outdoors. In humans, Neuroticism has been associated with decreased empathy, more authoritarian and over-protective parenting, as well as the provision of harshly controlled, but poorly structured, environments [79][80][81]. It is therefore important to determine if similar dynamics might be present in human-cat relationships, given that harsher, more forceful, and less predictable formal handling and husbandry styles have been associated with more negative wellbeing outcomes for cats [82][83]. While comparable studies in the domestic dog [84][85] reported similar owner-Neuroticism-pet-wellbeing relationships to those in [37], the current evidence base remains primarily correlational rather than causal (and based on subjective owner reports). Therefore, further investigations

examining the causal mechanisms underpinning the relationships between owner personality, human-cat interactions and cat wellbeing are needed.

7. The Ontogeny of Human and Conspecific Sociability in Cats Managed by Humans in Confined Environments

Positive human-social experiences during early developmental periods appear important predictors of friendliness (and its generalisation) towards humans later in life. Two studies ^{[86][87]} have investigated the effect of kittens being handled by humans during different periods of their development (e.g., from 1–5 weeks of age, or from 2–6 weeks, 3–7 weeks, or 4–8 weeks), and for different amounts of time each day (e.g., 15 min versus 40). The authors reported that kittens handled within the 2–7 week time period were generally more amenable to being handled and were quicker to approach people, as were those that were handled for longer periods each day. This 2–7 week 'sensitive period' was identified as the stage where kittens were deemed most receptive to social learning regarding humans, with handling commencing towards the later stages of this period reported to produce less effective results. Increased handling following a specific 'socialisation and habituation' programme (as opposed to more basic, limited handling) within a shelter context was also found to produce cats that were reported as displaying less fear-based behaviours towards their adoptive owners, as well as providing them with more 'social support' when assessed at a year of age ^[31]. In addition to the timing, quality, and quantity of handling, the number of different handlers may also impact on kittens' subsequent behaviour towards unfamiliar humans. In one study, kittens regularly handled by five different people (as opposed to a single person or not handled at all) were observed to make fewer attempts to retreat from a stranger ^[88].

8. Lifestyle Variation, Social Flexibility, and Welfare Considerations

Within a cats' lifetime, some individuals may transition from an independent free-living lifestyle to cohabiting with humans (and also conspecifics) within the confines of a domestic home. In some instances, the cat might actively facilitate this transition, for example they may start spending time near to human dwellings and eventually decide to 'move in'. In most cases, however, this process occurs due to human intervention. Typically, a cat deemed to be 'stray' or 'unowned' is physically removed from its original location, temporarily housed in a shelter environment, before then being placed into a domestic home of humans' choosing. Indeed, such cats can represent a large proportion of the total shelter population, with a UK study suggesting up to as many as 42% within a given year ^[89]. It is worth noting that prior to a period of free living, some of these stray or unowned cats may have originated from domestic homes, and thus been appropriately socialised (to humans and potentially conspecifics) during their sensitive period. However, many of these free-living cats may have had no, or very limited, social experiences with either species, and thus potentially a much more limited capacity to adapt well to future environments that require close cohabitation with them.

Within the shelter environment, a cats' previous social experiences (and inferred degree of socialisation) appear to be important determinants of their wellbeing. In ^[39] cats that were deemed to be 'unsocialised' towards humans had higher Cat Stress Scores (CSS) than those considered to be 'socialised', and those considered 'unsocialised' to conspecifics had higher CSS when housed in groups. In another study ^[40], cats that had previously resided in single, rather than multi-cat, homes were found to have significantly higher CSS during the first few days of their arrival at a shelter, even though they were housed individually. A lack of previous socialisation to humans and conspecifics is therefore likely to compromise the wellbeing of cats when housed within a shelter environment. While the impact of conspecifics on cats unsocialised to cats can potentially be mitigated by providing them with single housing, an equivalent is obviously more difficult to provide for cats unsocialised to humans within such human-managed confined environments. Comparable data regarding the wellbeing of cats within the domestic home, based on their lack of previous socialisation to humans and/or cats, is missing. However, it is anticipated that similar relationships are likely present, with such previously unsocialised cats struggling more (or generally failing) to adapt.

Potentially heritable traits may also interact with kittens' early social experiences to impact the nature of their social behaviour towards humans. Cats' social experiences with conspecifics during their sensitive period appear similarly important in influencing subsequent social behaviour towards other cats. Under certain conditions, such as limited amounts of human-socialisation and barren environmental conditions, impacts of a cats' early social environment on their subsequent behaviour towards humans may be subsumed by paternal genetic effects.

In general, adequate social exposure towards humans during the cats' sensitive period (i.e., 2–7 weeks of age) and beyond, appear central to the development and stability of human-sociability, although inherited traits (e.g., boldness/shyness) may also play important mediating roles. Later separation (i.e., beyond the cats 'sensitive period' for human-socialisation) from mother and siblings may also enhance both conspecific and human-cat social relationships

later in life. Related conspecifics that remain together from birth may be more likely to engage in affiliative interactions than non-related cohabiting conspecifics. However, whether cats have a similar 'sensitive period' for the development of sociability to conspecifics, if this generalises to unfamiliar, unrelated cats in the same way that it might in humans, and the role of heritable personality traits as moderating factors remain unclear.

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