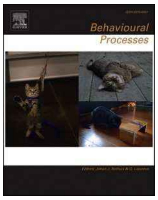
Behavioural Processes 213 (2023) 104959

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Feline faces: Unraveling the social function of domestic cat facial signals

Lauren Scott [a], Brittany N. Florkiewicz [b,*]

[a] *School of Medicine, University of Kansas Medical Center, KS, USA*
[b] *Department of Psychology, Lyon College, Batesville, AR, USA*

ARTICLE INFO

Keywords:
Domestic cat
Facial signals
Sociality
Communication
Compositionality
Complexity

ABSTRACT

Lately, there has been a growing interest in studying domestic cat facial signals, but most of this research has centered on signals produced during human-cat interactions or pain. The available research on intraspecific facial signaling with domesticated cats has largely focused on non-affiliative social interactions. However, the transition to intraspecific sociality through domestication could have resulted in a greater reliance on affiliative facial signals that aid with social bonding. Our study aimed to document the various facial signals that cats produce during affiliative and non-affiliative intraspecific interactions. Given the close relationship between the physical form and social function of mammalian facial signals, we predicted that affiliative and non-affiliative facial signals would have noticeable differences in their physical morphology. We observed the behavior of 53 adult domestic shorthair cats at CatCafé Lounge in Los Angeles, CA. Using Facial Action Coding Systems designed for cats, we compared the complexity and compositionality of facial signals produced in affiliative and non-affiliative contexts. To measure complexity and compositionality, we examined the number and types of facial muscle movements (AUs) observed in each signal. We found that compositionality, rather than complexity, was significantly associated with the social function of intraspecific facial signals. Our findings indicate that domestication likely had a significant impact on the development of intraspecific facial signaling repertoires in cats.

1. Introduction

Mammalian cranial morphology is comprised of distinct features (Higashiyama et al., 2021; Usui and Tokita, 2018; Caro, 2009) and elaborate underlying musculature (Brecht and Freiwald, 2012; Waller et al., 2020; Diogo et al., 2009) which has paved the way for more complex forms of visual signaling (Brecht and Freiwald, 2012; Darwin, 1872; Santana et al., 2014). Individual facial muscle movements are combined to create facial signals that vary in physical form (Waller et al., 2020; Waller and Micheletta, 2013) and social function (Clark et al., 2020, 1860; Waller et al., 2015; Waller and Dunbar, 2005; Waller et al., 2016) among mammals. Consequently, mammalian facial signal repertoires vary according to their socio-ecologies (Waller and Micheletta, 2013; Florkiewicz et al., 2023; Scheider et al., 2014, 2016; Florkiewicz et al., 2018). For example, relaxed open-mouth faces have been documented in carnivores (Davila-Ross and Palagi, 1863; Taylor et al., 2019; Palagi et al., 2019a; Maglieri et al., 2022; Llamazares-Martín et al., 2017), odd-toed ungulates (Maglieri et al., 2020; Schilder et al., 1984), and primates (Palagi et al., 2019b; Mancini et al., 2013; Palagi, 2008; Davila-Ross et al., 2015; Davila Ross et al., 2008; Palagi et al., 2014; Zhang et al., 2019) that engage in frequent bouts of social play (Davila-Ross and Palagi, 1863; Preuschoft and van Hooff, 1997). The relaxed open-mouth is morphologically distinct from other facial signals (Davila-Ross and Palagi, 1863; Davila-Ross et al., 2015) and serves to modulate play type and intensity (Davila-Ross and Palagi, 1863; Palagi, 2008; Davila-Ross et al., 2015; Gallo et al., 2022; Ross et al., 2014). Domestication often leads to alterations in mammalian socio-ecologies (Kaiser et al., 2015; Cordoni and Palagi, 2019; Kortekaas and Kotrschal, 2019; Range and Marshall-Pescini, 2022) and has the potential to influence their facial signaling repertoires. Domesticated dogs, for example, exhibit greater mobility of the inner brow compared to wolves (Kaminski et al., 2019), which enhances the neonatal appearance of their facial signals (Waller et al., 2013c).

Like domesticated dogs, the domestic cat (*Felis silvestris catus*) has experienced significant socio-ecological changes due to domestication. In recent years, there has been increased interest in studying domestic cat facial signals to improve their welfare. Facial muscle movements produced during pain have been used to establish assessment scales

---

* Corresponding author.
E-mail address: Brittany.florkiewicz@lyon.edu (B.N. Florkiewicz).

https://doi.org/10.1016/j.beproc.2023.104959
Received 13 August 2023; Received in revised form 12 October 2023; Accepted 15 October 2023

(Evangelista et al., 2019; Reid et al., 2018; Steagall and Monteiro, 2019) and automated recognition systems (Feighelstein et al., 2022) for domesticated cats. Facial signals directed toward humans have been used to infer the emotions of domesticated cats (Bennett et al., 2017; Dawson et al., 2019) and assess their adoption rates (Caeiro et al., 2017). Most current research on domesticated cats has focused on facial signals elicited through emotional arousal (Evangelista et al., 2019; Reid et al., 2018; Steagall and Monteiro, 2019; Bennett et al., 2017) or human-cat interactions (Bennett et al., 2017; Dawson et al., 2019; Caeiro et al., 2017). However, domesticated cats have flexible social structures that often involve intraspecific interactions. Our current study examines the physical form and social function of domestic cat facial signals that are produced during intraspecific social interactions. By doing so, we will better understand how domestication has shaped the communicative abilities of cats.

1.1. *Sociality & communication*

The social organization of the domestic cat is highly flexible that can influence the quantity and quality of intraspecific interactions. Many households consist of a single cat (Larkin and Radich, 2021), although multi-cat households are commonly observed (Khoddami et al., 2023; Bernstein and Strack, 1996; Elzerman et al., 2020). In shelters, cats can be housed in isolation or in groups of up to 50 individuals (Gouveia et al., 2011; Loberg and Lundmark, 2016; Kessler and Turner, 1999) that vary concerning their age, breed, sex, and relatedness (Khoddami et al., 2023). In the outdoors, free-ranging cats are found in locations spanning from parking lots to islands (Vitale, 2022a). Population densities of free-ranging cats can vary from 1 to 2500 individuals/km^2 (Vitale, 2022a; Liberg et al., 2000). Free-ranging cats are facultatively social and often congregate into matrilineal colonies comprised of queens, their offspring, and relatives (Vitale, 2022a; Crowell-Davis et al., 2004). Colonies are sometimes cared for through the cooperation of human caregivers, although some colonies live free from human contact (Vitale, 2022a). The closest living relatives of domesticated cats (*F. s. silvestris, F. s. lybica, F. s. ornata, F. s. cafra, and F. s. bieti;* (Yamaguchi et al., 2004); Driscoll et al., 2011; Yu et al., 2021) are solitary-living (Cafazzo and Natoli, 2009; Bradshaw, 2016), which suggests that their flexible social organization has been more recently acquired. Intraspecific sociality could have been favored as access to food increased around human settlements (that also provided greater protection against predators; (Bradshaw, 2016)). Consequently, a greater reliance on intraspecific facial signaling may be observed.

Cat intraspecific social interactions are categorized into four main contexts: affiliative, non-affiliative, caregiving, and reproductive (Vitale, 2022a; Crowell-Davis et al., 2004; Bradshaw, 2016). Affiliative interactions often involve allogrooming and allorubbing that aid in social bond management (Crowell-Davis et al., 2004; Bradshaw, 2016). Allogrooming is performed unidirectionally by mothers to their offspring but is reciprocal among adults (Bradshaw, 2016; Brown and Bradshaw, 2014). In contrast, allorubbing is directed from younger to older age classes (Bradshaw, 2016). Bodily contact during rest, nose sniffing, vertical tail positioning, and play have also been noted as affiliative behaviors produced by both kittens and adults (Vitale, 2022a; Crowell-Davis et al., 2004; Cafazzo and Natoli, 2009; Dards, 1983). Non-affiliative interactions can include assessment-related behaviors (staring and cautious approaches), defensive postures (fleeing, stiffening, piloerection), and aggressive exchanges (biting, growling, hissing, scratching, spitting, and swatting) (Yeon et al., 2011; Natoli et al., 2001; Stelow et al., 2016; Penar and Klocek, 2018). Non-affiliative interactions occur among all age groups and are often the result of territorial disputes (in both free-ranging and household cats; (Elzerman et al., 2020); Loberg and Lundmark, 2016; Bradshaw, 2016). Caregiving involves affiliation performed by mothers to their offspring (mainly through allogrooming) along with nursing and communal denning (Vitale, 2022a; Bradshaw, 2016; Vitale, 2022b). Reproductive behaviors are restricted to adults, and involve mounting and copulation.

Current evidence indicates that facial signals play a key role in navigating non-affiliative intraspecific interactions. In defensive posturing, the ears are flattened and the teeth are exposed, whereas in aggressive exchanges, the ears are narrow and rotated to the side (Bennett et al., 2017; Brown and Bradshaw, 2014). Variability has been demonstrated in these displays (Bennett et al., 2017) through blending (i.e., combining two or more facial signal types) and grading (i.e., modifying intensity and morphology) (Parr et al., 2005), which in turn increases their repertoire size. Few studies have focused on facial signals produced during affiliative, caregiving, and reproductive interactions among conspecifics, since it is assumed that facial signaling is *"mainly used in regulating aggressive behavior"* (Brown and Bradshaw, 2014), p. 51. The history of domestication could provide clues to the greater number of defensive and aggressive facial signals used by cats. Compared to dogs (Parker et al., 2010), cat domestication has taken place for a relatively short amount of time (around 10,000 years; (Montague et al., 2014)) that could result in minimal changes to their facial signaling repertoires (Caeiro et al., 2017; Brown and Bradshaw, 2014). The closest living relatives of domesticated cats (wildcats) are territorial and are likely to use non-affiliative facial signals for resolving disputes (Cafazzo and Natoli, 2009; Bradshaw, 2016). Wildcats are solitary mammals that tend to avoid both humans and conspecifics (outside of the mating season; (Berteselli et al., 2017); Beugin et al., 2016). While domestic cats have adapted to a more varied diet, wildcats are facultative carnivores that prey upon small-bodied mammals (Berteselli et al., 2017; Dickman, 1996). Wildcats establish hunting territories that seldom overlap, while domesticated cats frequently overlap territories (but hunt alone; (Corbett, 1979)). Wildcats also produce territorial behaviors, such as scent-marking and vigilance postures, more often than domesticated cats (Berteselli et al., 2017). These non-affiliative facial signals may have been preserved among domesticated cats (who often engage in aggressive interactions; (Elzerman et al., 2020); Gouveia et al., 2011; Dantas-Divers et al., 2011; Wagner et al., 2018).

However, domesticated cats display greater social tolerance and engage in more affiliative behaviors than wildcats, including play, social resting, grooming, and allorubbing (Berteselli et al., 2017). The transition to intraspecific sociality among domesticated cats could also result in a greater reliance on affiliative facial signals that aid in reducing stress and strengthening bonds. Examples from other mammals include lip smacking (Fedurek et al., 2015; Maestripieri and Wallen, 1997; van de Waal et al., 2013), chattering (Palagi and Mancini, 2011), and play faces (Davila-Ross and Palagi, 1863; Taylor et al., 2019; Palagi et al., 2019a; Maglieri et al., 2022; Llamazares-Martín et al., 2017; Maglieri et al., 2020; Schilder et al., 1984; Palagi et al., 2019b; Mancini et al., 2013; Palagi, 2008; Davila-Ross et al., 2015; Davila Ross et al., 2008; Palagi et al., 2014; Zhang et al., 2019), which are used to modulate affiliative activities (play and grooming) and are associated with social bonding. Strong social bonds have a positive impact on the inclusive fitness of the domesticated cat. For example, adult females with strong social bonds exhibit alloparenting behavior, which is crucial for the survival of their offspring (Vitale, 2022a). Affiliative facial signals could therefore have important fitness consequences for domesticated cats. Given the close relationship between the physical form and social function of mammalian facial signals, the affiliative facial signals produced by domesticated cats during intraspecific interactions are likely to be morphologically distinct from their non-affiliative counterparts (Waller et al., 2020; Waller and Micheletta, 2013).

1.2. *Current study*

The goal of our study was to document facial signals produced by domesticated cats (*Felis silvestris catus*) during intraspecific social interactions. With the transition to greater levels of intraspecific sociality and affiliation (facilitated by domestication), we predicted differences in the physical form of facial signals based on their social function (affiliative vs. non-affiliative). Our study is unique in that it focuses on intraspecific, rather than interspecific, facial signals produced in both affiliative and non-affiliative contexts.

Following previous studies, we assessed differences in the physical form of facial signals using Facial Action Coding Systems (or FACS) specifically designed for cats (catFACS; (Caeiro et al., 2017, 2013a). FACS are systematic and standardized tools for the study of human and non-human facial signals (Florkiewicz et al., 2023; Parr et al., 2010). Users are trained to identify subtle and overt facial muscle movements (which are referred to as action units or AUs) that are combined to create a signal (AU combination) (Ekman and Rosenberg, 2005a). By placing equal emphasis on all AUs, the risk of observational bias is minimized (Florkiewicz et al., 2023; Ekman and Rosenberg, 2005a). Previous studies on cat social behavior have often used ethograms to categorize facial signals and other social behaviors (Brown and Bradshaw, 2014; Leyhausen, 1979). While behavioral ethograms are useful for discretization and rate calculations (Asher et al., 2009), they run the risk of oversimplifying facial signaling repertoires. For example, facial signaling ethograms for chimpanzees (*Pan troglodytes*) and hylobatids (family Hylobatidae) are often comprised of 4–10 discrete signal types (Parr et al., 2007; Florkiewicz and Campbell, 2021a; Liebal et al., 2004). But recent studies have found that chimpanzees and hylobatids are capable of producing up to 357 and 80 morphologically distinct facial signals, respectively (Florkiewicz et al., 2023). By using the catFACS, we can better understand how social function influences the physical formation of intraspecific facial signals. Recent studies on cat facial signaling have been able to successfully utilize catFACS to develop pain assessment tools (Evangelista et al., 2019; Reid et al., 2018; Steagall and Monteiro, 2019; Feighelstein et al., 2022), infer emotions (Bennett et al., 2017), and examine factors influencing adoption rates (Caeiro et al., 2017).

Past studies have used the FACS to assess the physical form of facial signals using two measures: complexity and compositionality. The total number of individual AUs in combinations has been used to evaluate complexity (Florkiewicz et al., 2023; Scheider et al., 2014; Florkiewicz et al., 2018), whereas compositionality is evaluated based on the presence/absence of certain AUs within a combination (Florkiewicz et al., 2023); Bennett et al. (2017); Caeiro et al. (2017); Parr et al. (2007). It is also possible that complexity and compositionality are influenced not just by a species' socio-ecology, but also by the types of social interactions they engage in (Florkiewicz et al., 2023; Oña et al., 2019). Using these measures, we generated the following two predictions for domestic cat intraspecific facial signals:

Prediction 1 (P1): Affiliative and non-affiliative facial signals should differ in complexity (i.e., the number of AUs used to produce a facial signal). Domesticated cats have a more complex and variable social organization when compared to wildcats (Berteselli et al., 2017; Beugin et al., 2016). Communicative complexity has been linked to social complexity and enables affiliative behaviors (such as cooperation and reconciliation; (Freeberg and Krams, 2015)). For this reason, we predict that affiliative facial signals should be more complex than non-affiliative signals.

Prediction 2 (P2): Affiliative and non-affiliative facial signals should differ in compositionality (i.e., types of AUs used to produce a facial signal), since the information conveyed by each signal type should be different.

Pet owners and shelters can use our findings to increase the probability of successful bonding between domesticated cats. Conflict behaviors are frequently reported among multi-cat households (Elzerman et al., 2020) and shelters where cats are housed in groups (Gouveia et al., 2011; Dantas-Divers et al., 2011; Wagner et al., 2018). One previous study found that providing more space for cats to roam can encourage affiliative intraspecific behaviors (Loberg and Lundmark, 2016), but this may not always be feasible. In these instances, introduction and observation plans are critical for bonding success (Cummings, 2019). Recognizing the difference between affiliative and non-affiliative facial signals can be helpful in recognizing signs of tension and mediating conflicts.

2. Methods

2.1. Data collection

Our study took place at the CatCafé Lounge, a non-profit rescue organization in Los Angeles, CA. The CatCafé Lounge was established in 2018 to increase cat adoption rates through intra- and inter-specific socialization. The lounge features an open indoor floor plan where visitors can interact with approximately 20–30 group-housed cats that are available for adoption. During the warmer months, cats and humans can also interact in a fenced-in outdoor patio area connected to the lounge (referred to as the 'catio'; Fig. 1). Cats are given ad libitum access to food, water, litter boxes, and a variety of enrichment items (scratching posts, wooden perches, hidden nooks, and toys) in the indoor lounge and patio area. All cats have the option to withdraw from humans and other cats by finding shelter in the back room or hidden areas. Daily cleaning is performed by staff before and after visiting hours. Our study was approved by the CatCafé Lounge and was conducted in accordance with the NC3R's ARRIVE guidelines and the Association for the Study of Animal Behaviour's guidelines for the treatment of animals in behavioral research (No authorship, 2020). Because our study made use of non-invasive behavioral observations (that were recorded in staff and visitor viewing areas), full IACUC approval was waived for this study.

During our study, new cats were introduced to the group, allowing us to increase the size of our subject pool. Before new cats are granted access to the lounge and catio, they are assessed by a veterinarian and quarantined for observation. Once a new cat gains medical clearance (i.e., is vaccinated, spayed/neutered, and shows no signs of illness) from the veterinarian and lounge staff, they are moved to a larger socialization room. New cats can interact with other group-housed lounge cats in the socialization room under staff supervision. After 2–3 days, the new cat is granted full access to the CatCafé Lounge, including the indoor lounge area and catio. Cats who have access to the indoor lounge and catio can freely interact with other cats at any time, which allowed us to observe a wide variety of intraspecific communicative events.

We collected our data from August 2021 to June 2022 across 150 visiting hours. Over the 10 months, we were able to observe the facial signaling behavior of 53 adult domestic short-haired cats ($\geq$1 year). Introduction and adoption timelines varied; some cats were present for the entire 10-month period, whereas others were only present for a few weeks. Our sample consisted of 27 females and 26 males that were all spayed/neutered. Information regarding the names and sexes of the cats incorporated into our study can be found in the electronic supplement (Table S1). We excluded kittens from our study (<1 year) since adulthood is typically associated with greater behavioral stability (Travnik et al., 2020). Kittens were also housed in a separate lounge from adult cats as a health precaution. Data were collected in the form of video recordings after visiting hours (5:30 – 8:30 PM) to maximize the probability of observing intraspecific (rather than interspecific) communicative events. Video recordings were taken by the first author (LS). Most video recordings took place in the lounge and catio (Fig. 1), although some videos were also taken in the socialization room (if an interaction was observed). Video recordings were taken with a Panasonic Full HD Video Camera Camcorder HC-V770 using the opportunistic sampling method, which previous studies have found effective for increasing facial signal sample sizes (Florkiewicz and Campbell, 2021b). We followed the most active group of cats and took video recordings just before the start of a communicative event using our camcorder's pre-record function. Video recordings ended when cats either dispersed and/or ceased communicating with one another.

Fig. 1. Our study took place at the CatCafé Lounge. We collected data in two main areas, which include the indoor lounge (top image) and catio (bottom image). Cats can freely interact with conspecifics and humans in these areas.

2.2. Data coding

In our current study, we defined a facial signal as facial muscle movement(s) that a cat produces during a communicative event (Florkiewicz et al., 2023; Smith and Harper, 1995). To accurately code signals directed at conspecifics, we coded facial signals only when the signaler's eyes and body were aimed towards the intended recipient(s). Our definition of a facial signal does not include facial muscle movement (s) associated with biological maintenance (such as breathing, mastication, or yawning) (Florkiewicz et al., 2023). Head and eye movements were not included in our study, since it was difficult to discern whether they were being used for communication. We coded only facial signals that were directed toward conspecifics; we did not code facial signals that were produced toward humans or inanimate objects. Each facial signal was coded using the cat Facial Action Coding System (or catFACS) (Caeiro et al., 2013a). All facial signals were coded at their apex or 'production peak' (Florkiewicz et al., 2018). Following the language of the catFACS tool, we refer to individual facial muscle movements as action units (or AUs). Each facial signal was assigned a numerical combination (or AU combination) that contained information on the observed AUs (Caeiro et al., 2013a; Ekman and Rosenberg, 2005a). A list of all AUs that were considered can be found in the electronic supplement (Table S2). For each facial signal, we also coded: (1) the identity of the signaler; and (2) whether the signal occurred in a positive (affiliative) or negative (non-affiliative) context (Oña et al., 2019). Domestic cat social behaviors are often characterized into four main contexts: affiliative, non-affiliative, caregiving, and reproductive (Vitale, 2022a; Crowell-Davis et al., 2004; Bradshaw, 2016). We classified facial signals into two of these contexts (affiliative and non-affiliative). All adults were spayed/neutered prior to their introduction into the group, limiting opportunities for observing reproductive-related facial signals. Kittens were housed separately from adults, which also limited opportunities for observing caregiving-related facial signals. We assigned contexts by looking for accompanying behaviors that are often associated with affiliation and non-affiliation interactions in domesticated cats. Examples of affiliative behaviors in cats include allogrooming, allorubbing, bodily contact during rest, mating, nose sniffing, social rolling, play, and/or vertical tail positioning (Vitale, 2022a; Crowell-Davis et al., 2004; Vitale, 2022b). Examples of non-affiliative behaviors in cats include biting, fleeing, growling, hissing, piloerection, scratching, spitting, staring, and/or swatting (Stelow et al., 2016; Penar and Klocek, 2018). When assigning behavioral contexts, we considered the behavior of both the signaler and their intended recipient(s).

All variables were coded using ELAN 6.50AVFX (Lausberg and Sloetjes, 2009) with a custom coding template that can be found in the Electronic Supplement.

2.3. Agreement

To become certified in the use of catFACS, researchers are required to take a coding test and achieve an average Wexler's ratio of ≥ 0.70 with a member of the catFACS development team (Caeiro et al., 2013a). Both authors (LS and BF) were certified in catFACS before data coding in 2023. BF passed the catFACS test with a score of 0.756 in September 2021, and LS passed with a score of 0.717 in March 2022. We also assessed average agreement for 10% of our coded video clips using the same requirements that are needed to pass the catFACS test. Our average Wexler's ratio was 0.707, which is considered good agreement. We also assessed the percentage of agreement for the context of each facial signal (affiliative or non-affiliative). In previous facial signaling studies with mammals, percentage of agreements above 70% were considered good agreement (Florkiewicz and Campbell, 2021a). We agreed on the context for 75% of the facial signals sampled for assessment. When we were coding facial signaling contexts, we considered the actions of both the signalers and the recipients. However, disagreements in contexts may have arisen due to different behaviors exhibited by the signaler and the recipient. Social interactions may also transition between behavioral contexts, making specifying only one context type difficult. FACS and context coding was carried out by BF; LS independently coded 10% of all video clips to assess agreement.

2.4. Data analysis

We performed our statistical tests in R 4.1.0 (Team, R.C, 2021). Our behavioral data and R code can be found in the Electronic Supplement. To examine whether differences in the physical morphology of cat facial signals could be explained by differences in their social function, we compared facial signals produced in affiliative and non-affiliative contexts regarding their complexity (P1) and compositionality (P2). If differences in the physical morphology of cat facial signals can be explained by differences in social function, then we should see significant differences in: (P1) the number of AUs used to produce a facial signal in each context type; and/or (P2) the production of individual AUs in each context type.

For our analyses, we made use of generalized linear mixed models (GLMMs) to account for idiosyncrasies in facial signaling and the pooling fallacy (since each cat contributed multiple facial signals to our dataset; (Waller et al., 2013a)). In our full models, context was set as fixed effect and signaler ID was set as a random effect. We compared each of our full models to a null counterpart where only signaler ID (not context) was included as a random effect to determine if context had a significant influence ($p < 0.05$) on each AU. Comparisons between full and null models were made using a likelihood-ratio test using the ANOVA function in base R (Waller et al., 2013a).

For assessing the complexity of facial signals (P1), we implemented an ordinal GLMM with a logit link function using the "ordinal" package (Christensen and, September 14, 2019, 2021). Our outcome variable was set as the number of AUs present within a facial signal, which resulted in a naturally ordered category (with each step of complexity consisting of an additional AU; (Florkiewicz et al., 2023)). Although AU combinations may vary, they can be naturally group (and ordered) based on the number of AUs they contain. To examine the composition of facial signals (P2), we ran binomial GLMMs with a logit link function for each AU with at least 10 observations. We set the presence/absence of the AU in each facial signal as our outcome variable. Models for each AU were implemented using the "lme4″ package (Bates et al., 2015). Odds ratios (OR), in addition to model outputs, are presented for models where context had a significant influence on complexity/compositionality.

3. Results

Using the opportunistic sampling method, we were able to gather 194 min of video footage that featured 186 communicative events. In these communicative events, we coded 688 facial signals (413 that were produced by males and 275 by females). Out of the 688 coded facial signals, 354 (51.45%) were produced in an affiliative context and 334 (48.55%) were produced in a non-affiliative context. We observed 26 distinct AUs that were used to produce a total of 276 distinct AU combinations. A list of observed AU combinations and their frequencies can be found in the electronic supplement (Table S3). Only 48 (17.39%) of distinct AU combinations were observed in both affiliative and non-affiliative contexts; the remaining 228 were produced exclusively in either an affiliative (N = 126 or 45.65%) or non-affiliative (N = 102 or 36.96%) context.

3.1. Facial signaling complexity (P1)

On average, facial signals were comprised of 3.903 AUs (SD=2.166). The average number of AUs was slightly lower in affiliative facial signals (M=3.873, SD=2.102) when compared to non-affiliative facial signals (M=3.934, SD=2.234), but these differences were not statistically significant. Our ordinal GLMM containing context as a fixed effect was a poor fit compared to our null model ($ß=-0.480$, SE=0.148, $p = 0.746$).

3.2. Facial signaling compositionality (P2)

Across 688 facial signals, we coded a total of 2628 AUs. A list of observed AUs and their frequencies can be found below in Table 1.

Except for AD190 (tongue downwards), all observed AUs were found in both affiliative and non-affiliative contexts. Context had a significant influence on the production of 6 distinct AUs (Table 2). These included lip wipe (AD37), ear movements (EAD101, EAD102, EAD103, EAD104), and eye closure (AU143). AD69 (pupil constriction) and AU201 (whiskers forward) were very close to significance and are also included in Table 2. The remaining 17 AUs were not significantly influenced by context.

Ears forward (EAD101), ear adductor (EAD102), eye closure (AU143), and whiskers forward (AU201) were significantly associated with affiliative facial signals, whereas lip wipe (AD37), ear flattener (EAD103), ear rotator (EAD104), and pupil constriction (AD69) were significantly associated with non-affiliative facial signals (Fig. 2).

Table 1

In our study, we coded the AUs produced by 53 adult domestic shorthair cats. The frequency of each AU observed is presented along with the proportion of observations (out of the 2628 coded AUs) in the last column.

AU Code	AU Description	Frequency	Proportion of Obs.
EAD104	Ear Rotator	399	15.18%
EAD102	Ear Adductor	277	10.54%
EAD101	Ears Forward	222	8.45%
AU5	Upper Lid Raiser	218	8.30%
EAD103	Ear Flattener	184	7.00%
AU25	Lips Part	182	6.93%
AU26	Jaw Drop	163	6.20%
AU47	Half Blink	163	6.20%
AD68	Pupil Dilator	138	5.25%
AD69	Pupil Constrictor	135	5.14%
AU12	Lip Corner Puller	111	4.22%
AU116	Lower Lip Depressor	66	2.51%
AD137	Nose Lick	64	2.44%
EAD105	Ears Downward	63	2.40%
AU109 + 110	Nose Wrinkle & Upper Lid Raiser	56	2.13%
AU143	Eyes Closed	54	2.05%
AU201	Whisker Protractor	26	0.99%
AU200	Whisker Retractor	23	0.88%
AU27	Mouth Stretch	19	0.72%
AU202	Whisker Raiser	18	0.68%
AD37	Lip Wipe	14	0.53%
AD190	Tongue Downwards	9	0.34%
EAD106	Ears Backwards	9	0.34%
AD19	Tongue Out	6	0.23%
EAD107	Ears Constrictor	6	0.23%
AU145	Blink	3	0.11%

Table 2
The outputs of our binomial GLMMs. The presence/absence of each AU (in each facial signal) was set as our outcome variable. Context and signaler ID are set as fixed effects (with signaler ID as a random variable). Odds ratios (OR) are presented for each model in the last column. Non-affiliative is abbreviated as non-affil. Negative ß values for non-affil. indicate that each AU is more likely to appear in affiliative contexts, while positive ß values indicate the opposite.

AU Code	AU Description	Predictor Variable	ß	SE	z value	p-value	OR (Affiliative / Non-affil.)
AD37	Lip Wipe	(Intercept)	-4.762	0.580	-8.213	.000	0.251
		Non-affil.	1.382	0.656	2.108	.035	
AD69	Pupil Constrictor	(Intercept)	-2.127	0.337	-6.319	.000	0.599
		Non-affil.	0.512	0.261	1.958	.050	
EAD101	Ears Forward	(Intercept)	-0.497	0.158	-3.140	.001	1.785
		Non-affil.	-0.580	0.186	-3.118	.001	
EAD102	Ear Adductor	(Intercept)	-0.241	0.197	-1.224	.221	1.533
		Non-affil.	-0.428	0.188	-2.278	.022	
EAD103	Ear Flattener	(Intercept)	-1.487	0.198	-7.498	.000	0.585
		Non-affil.	0.537	0.199	2.701	.007	
EAD104	Ear Rotator	(Intercept)	-0.023	0.154	-0.153	.879	0.533
		Non-affil.	0.629	0.176	3.581	.000	
AU143	Eyes Closed	(Intercept)	-2.163	0.267	-8.093	.000	8.316
		Non-affil.	-2.118	0.455	-4.651	.000	
AU201	Whisker Protractor	(Intercept)	-3.575	0.531	-6.732	.000	2.838
		Non-affil.	-1.043	0.537	-1.941	.052	

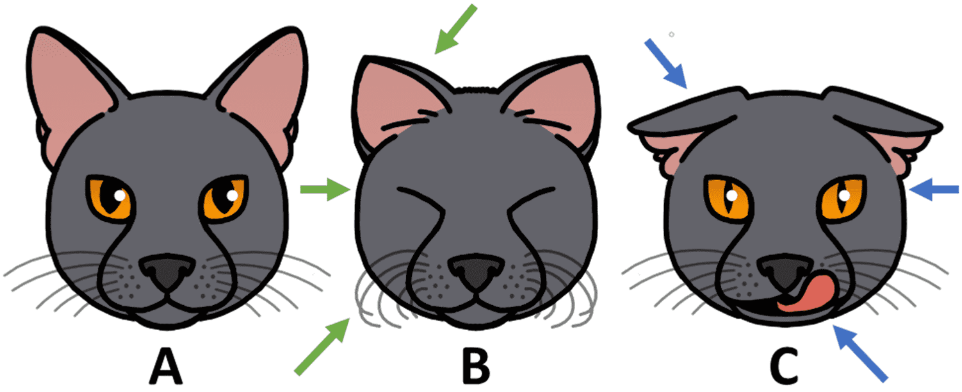


Fig. 2. An illustration of AUs that are significantly more likely to be produced in (B) affiliative contexts and (C) non-affiliative contexts. A neutral face is provided (A) for comparison. In affiliative facial signals (B), the ears are adducted (EAD102) and moved forward (EAD101), the whiskers are moved forward (AU201), and the eyes are closed (AU143). In non-affiliative facial signals (C), the ears are rotated (EAD104) and flattened against the head (EAD103), the pupils are constricted (AD69), and the lip is wiped with the tongue (AD37, which also requires AU25 and AU26/27). Illustration by Britt Florkiewicz.

4. Discussion

Our current study aimed to examine the facial signals produced by domesticated cats (*Felis silvestris catus*) during interactions with conspecifics. Because domestication has facilitated intraspecific sociality among cats, we predicted (P1 and P2) differences in the physical form of facial signals based on their social function (i.e., whether they are produced in affiliative or non-affiliative contexts). We assessed the physical form of facial signals using the number of AUs produced in each facial signal (P1) and the presence/absence of different AUs (P2).

We observed significant differences in the compositionality of facial signals produced in affiliative and non-affiliative contexts, providing support for our second prediction (P2). We identified eight facial muscle movements that differed between contexts, with half being associated with ear movements. During affiliative interactions, the ears are adducted and moved forward, whereas in non-affiliative interactions, the ears are rotated and flattened against the head. Movements of the eyes, tongue, and whiskers also differ in each context (Fig. 2).

The physical form of intraspecific facial signals could be attributed to mechanically effective behaviors. The physical form of affiliative facial signals may be associated with restful movements (eye closure) and movements facilitating auditory/tactile contact between conspecifics (ears and whiskers forward). In contrast, the physical form of non-affiliative facial signals could be associated with protective responses (Kiley-Worthington, 1976). Ear flattening and pupil constriction may be useful during agonistic encounters since the ears and retina are vulnerable to damage (Defensor et al., 2012; Mathôt, 2018). However, these facial muscle movements may also occur when the probability of bodily contact/fighting is low. Over time, the physical form of intraspecific facial signals could be subject to phylogenetic ritualization. During phylogenetic ritualization, mechanically effective behaviors are 'ritualized' into communicative signals within a given species (Tomasello and Call, 2019; Pika and Fröhlich, 2019). One example is the snarl of wolves, which was derived from facial muscle movements associated with biting behaviors (Pika and Fröhlich, 2019). These facial muscle movements can reduce the energy expenditure of the signaler while allowing recipients to make predictions about interaction outcomes (Waller et al., 2017). However, intraspecific facial signaling repertoires may also be subject to social transmission, ontogenetic processes, and/or social negotiation (Pika and Fröhlich, 2019). Additional comparative research is needed to discern how domestic cat intraspecific facial signaling repertoires are obtained.

The physical form of non-affiliative facial signals differs between intraspecific and interspecific social interactions. One previous study found that certain non-affiliative cat facial signals can indicate offensive or defensive behavior during human encounters. Offensive facial signals include ear rotation (EAD104), pupil construction (AD69), and the upper eyelid being raised (AU5), while defensive facial signals may involve ear flattening (EAD103), pupil dilation (AD68), mouth stretching (AU25 +27), and flashing the upper (AU109 +110) and lower

(AU116) rows of teeth (Bennett et al., 2017). We observed three of these movements (AD69, EAD103, and EAD104) in non-affiliative intraspecific facial signals. The remaining movements did not significantly differ between affiliative and non-affiliative contexts. One explanation for these observed differences is that cats use modified facial signaling repertoires when interacting with humans. Support for this idea comes from previous work on cat vocalizations. Cats vocalize more frequently to humans than other cats (Turner, 2017), and their vocalizations are also higher in pitch when directed at humans (Yeon et al., 2011). In our current study, we considered 29 facial muscle movements (AUs) but only observed 26. Movements not observed include chin raiser (AU17), lip pucker (AU118), and third eyelid show (AD48). It is possible that these facial muscle movements are not used during intraspecific interactions or that they are difficult to identify (due to their subtle appearance). Previous studies have encountered similar sampling issues with these facial muscle movements (Caeiro et al., 2017).

While our second prediction was supported, our first prediction (P1) was not: there were no significant differences in the complexity of facial signals produced in affiliative and non-affiliative contexts. Compared to other mammals (with FACS), cats have limited facial mobility (Waller et al., 2020). Limitations in facial mobility could limit the complexity of facial signals, regardless of context. However, the average number of AUs found in domestic cat facial signals (mean=3.903) is consistent with primates (who exhibit greater facial mobility; (Florkiewicz et al., 2023)). An alternative explanation is that the complexity of domestic cat facial signals is more closely connected to social organization than context. Previous studies with primates have linked the complexity of facial signals to group size, with larger groups producing more complex signals (Florkiewicz et al., 2023). When larger groups of individuals interact, they engage in a diverse range of affiliative and non-affiliative behaviors. Consequently, there may be similarities in the complexity of facial signaling in each context. This may also be the case with domesticated cats, who vary in group size and organization. The CatCafé Lounge typically houses 20–30 cats, which remained consistent in number throughout our study. When compared to smaller populations of cats (such as multi-cat households or free-ranging colonies), variation in facial signaling complexity could be observed in our present sample. Throughout our study, new cats were introduced and others were adopted out, impacting the composition of the group. Changes in the social group's composition can also lead to variation in facial signaling complexity. More research is needed to explore the link between group size, group composition, and facial signaling complexity in domesticated cats.

Overall, we found that cats can produce many morphologically distinct AU combinations (N = 276). Most of these AU combinations are exclusive to affiliative or non-affiliative contexts, which further suggests differences in social function. It is important to note that the number of observations for each distinct combination of AUs was relatively low; 94.95% of distinct AU combinations had fewer than 10 observations. Consequently, this limited our ability to run statistical analyses for AU combinations (that has been done in previous studies; (Florkiewicz et al., 2023)). Information on the number (and types) of distinct AU combinations can still be useful for future comparative studies (using FACS; (Waller et al., 2020); Parr et al., 2010; Ekman and Rosenberg, 2005b; Caeiro et al., 2013b; Correia-Caeiro et al., 2022, 2021; Julle-Danière et al., 2015; Waller et al., 2012; Wathan et al., 2015; Vick et al., 2007; Waller et al., 2013b). For example, previous research has revealed specific AUs that are associated with play faces such as AU12 (lip corner puller; (Davila-Ross and Palagi, 1863); Parr et al., 2007). We observed 139 distinct AU combinations that were produced during playful interactions (that we categorized as affiliative; Table S3). AU12 was observed in 48 of these distinct AU combinations and was accompanied by other AUs associated with play (such as AU16/116 lower lip depressor, AU25 lips part, and AU26/27 jaw drop/mouth stretch; (Davila-Ross and Palagi, 1863); Parr et al., 2007). These AU combinations may be associated with play faces, which could offer valuable insight into the widespread nature of mimicry and empathy (Palagi et al., 2019a; Maglieri et al., 2020; Palagi et al., 2019b; Mancini et al., 2013; Davila Ross et al., 2008; Gallo et al., 2022; Bresciani et al., 2022; Palagi et al., 2015; Scopa and Palagi, 2016).

Taken together, our findings indicate that domestic cat intraspecific facial signals are not exclusive to agonistic interactions. Domesticated cats can produce affiliative and non-affiliative facial signals that exhibit differences in their morphological composition. These results provide greater insight into the impact domestication has on facial signaling repertoires. As intraspecific sociality became more prevalent, cats may have incorporated affiliative facial signals into their repertoires. Using affiliative facial signals can be beneficial in situations where there is a higher likelihood of stress, conflict, and competition. For example, lip smacking (an affiliative facial signal produced by primates) is commonly deployed in stressful grooming situations to avoid conflict (van de Waal et al., 2013). Additional research is needed to understand the origins of these affiliative facial signals, as domestication has taken place for a relatively short amount of time (around 10,000 years; (Montague et al., 2014)). On one hand, the affiliative facial signals produced by domesticated cats during intraspecific interactions may be uniquely derived. It is also possible that other members of *Felis silvestris* produce affiliative facial signals towards conspecifics, which may have been further developed through selective breeding in domesticated cats.

4.1. *Study limitations and future directions*

Our results provide greater insight into the facial signaling abilities of domesticated cats, there are four limitations to our study. First, we focused on a single population of domesticated 'rescue' cats housed at the CatCafé Lounge in Los Angeles, CA. Although the number of cats remained consistent, group composition was unstable. To confirm whether our findings apply to all domesticated cats, future research is required with stable multi-cat households, cats residing in other shelters, and free-ranging populations. Second, our study focuses on the facial signaling repertoires of one cat species (*Felis silvestris catus*). To better understand the link between affiliative signaling and domestication, we should examine the facial signals of the domestic cat's closest living relatives (wildcat species *F. s. silvestris*, *F. s. lybica, F. s. ornata, F. s. cafra, and F. s. bieti;* (Yamaguchi et al., 2004; Driscoll et al., 2011; Yu et al., 2021). Developing FACS for wildcat species would be beneficial for conducting this future research. Third, we were unable to include additional demographic variables (such as exact age, genomic breed composition, and relatedness) in our study. The CatCafé Lounge is a non-profit organization that rescues cats from different sources. In many instances, it is not possible to discern demographic variables without additional genetic testing (t can be costly). While we focused on the behavior of adult (≥1 year) domestic short-hairs, future research is required to confirm the impact of other demographic factors. Fourth, and finally, we were unable to track the adoption timelines of cats included in our study. Since we made use of opportunistic sampling, shelter duration would have been useful for identifying differences in recording opportunities. Tracking adoption timelines would have also been useful for discerning group stability and social organization.

5. Conclusion

The process of domestication has led to a greater variety of intraspecific social interactions among cats. Domesticated cats often engage in non-affiliative interactions, but they also display numerous affiliative behaviors that are crucial for managing social bonds. The goal of our study was to document the various kinds of facial signals produced by domesticated cats during affiliative and non-affiliative interactions with conspecifics. Since the physical form of facial signals is often shaped by their social function in mammals, we predicted that affiliative facial signals would differ in complexity (prediction 1) and compositionality (prediction 2) compared to non-affiliative facial signals. We found that compositionality, but not complexity, was significantly associated with intraspecific facial signaling function. Our findings indicate that domestication likely had a significant impact on the development of affiliative facial signaling repertoires in cats.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of Competing Interest

The authors have no conflicts of interest to declare for the current study.

Data Availability

All data underlying the current study will be made available as Electronic Supplementary Material, in addition to the ELAN coding templates and R script.

Acknowledgements

We would like to thank the staff and volunteers at the CatCafé Lounge for access to their cat population and their invaluable insight on domestic cat behavior during data collection. We are grateful to Dr. Matthew Campbell at California State University Channel Islands for providing feedback on the theoretical framing of our manuscript, and Emersen Ross at Lyon College for providing suggestions for our literature review. We also thank members of the AnimalFACS research team for their aid with catFACS certification.

CRediT authorship contribution statement

Lauren Scott: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – review & editing. **Brittany N. Florkiewicz**: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – review & editing, Visualization, Supervision, Project administration.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2023.104959.

References

Asher, L., et al., 2009. Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. J. R. Soc. Interface 6 (41), 1103–1119.

Bates, D., et al., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48.

Bennett, V., Gourkow, N., Mills, D.S., 2017. Facial correlates of emotional behaviour in the domestic cat (Felis catus). Behav. Process. 141, 342–350.

Bernstein, P.L., Strack, M., 1996. A game of cat and house: spatial patterns and behavior of 14 domestic cats (Felis catus) in the home. Anthrozoös 9 (1), 25–39.

Berteselli, G.V., et al., 2017. European wildcat and domestic cat: do they really differ? J. Vet. Behav. 22, 35–40.

Beugin, M.-P., et al., 2016. Female in the inside, male in the outside: insights into the spatial organization of a European wildcat population. Conserv. Genet. 17.

Bradshaw, J.W.S., 2016. Sociality in cats: a comparative review. J. Vet. Behav. 11, 113–124.

Brecht, M., Freiwald, W.A., 2012. The many facets of facial interactions in mammals. Curr. Opin. Neurobiol. 22 (2), 259–266.

Bresciani, C., Cordoni, G., Palagi, E., 2022. Playing together, laughing together: rapid facial mimicry and social sensitivity in lowland gorillas. Curr. Zool. 68 (5), 560–569.

Brown, S.L., Bradshaw, J.W., 2014. Communication in the domestic cat: within-and between-species. Domest. Cat: Biol. Behav. 37–59.

Caeiro, C.C., et al., 2013b. OrangFACS: a muscle-based facial movement coding system for orangutans (Pongo spp.). Int. J. Primatol. 34 (1), 115–129.

Caeiro, C.C., Burrows, A.M., Waller, B.M., 2017. Development and application of CatFACS: are human cat adopters influenced by cat facial expressions? Appl. Anim. Behav. Sci. 189, 66–78.

Caeiro, C., B. Waller, and A. Burrows, 2013a. The Cat Facial Action Coding System manual (CatFACS).

Cafazzo, S., Natoli, E., 2009. The social function of tail up in the domestic cat (Felis silvestris catus). Behav. Process. 80 (1), 60–66.

Caro, T., 2009. Contrasting coloration in terrestrial mammals. Philos. Trans. R. Soc. B: Biol. Sci. 364 (1516), 537–548.

Christensen, R.H.B. Package 'ordinal'. 2019 [cited 2021 September 14]; Available from: ⟨https://github.com/runehaubo/ordinal⟩.

Clark, P.R., et al., 1860. Crested macaque facial movements are more intense and stereotyped in potentially risky social interactions. Philos. Trans. R. Soc. B: Biol. Sci. 2022 (377), 20210307.

Clark, P.R., et al., 2020. Morphological variants of silent bared-teeth displays have different social interaction outcomes in crested macaques (Macaca nigra). Am. J. Phys. Anthropol. 173 (3), 411–422.

Corbett, L.K., 1979. Feeding Ecology and Social Organization of Wildcats (Felis silvestris) and Domestic Cats (Felis catus) in Scotland. University of Aberdeen.

Cordoni, G., Palagi, E., 2019. Back to the future: a glance over wolf social behavior to understand dog-human relationship. Anim. (Basel) 9 (11).

Correia-Caeiro, C., et al., 2022. CalliFACS: the common marmoset facial action coding system. PLoS ONE 17 (5), e0266442.

Correia-Caeiro, C., Holmes, K., Miyabe-Nishiwaki, T., 2021. Extending the MaqFACS to measure facial movement in Japanese macaques (Macaca fuscata) reveals a wide repertoire potential. PLOS ONE 16 (1), e0245117.

Crowell-Davis, S.L., Curtis, T.M., Knowles, R.J., 2004. Social organization in the cat: a modern understanding. J. Feline Med. Surg. 6 (1), 19–28.

Cummings, D.L., 2019. Practical guidance on how to facilitate harmonious feline social interactions with conspecifics. Companion Anim. 24 (11), 556–560.

Dantas-Divers, L.M., et al., 2011. Agonistic behavior and environmental enrichment of cats communally housed in a shelter. J. Am. Vet. Med. Assoc. 239 (6), 796–802.

Dards, J.L., 1983. The behaviour of dockyard cats: interactions of adult males. Appl. Anim. Ethol. 10 (1–2), 133–153.

Darwin, C., 1872. The Expression of the Emotions in Man and animals. John Murray, London, England, p. 374.

Davila Ross, M., Menzler, S., Zimmermann, E., 2008. Rapid facial mimicry in orangutan play. Biol. Lett. 4 (1), 27–30.

Davila-Ross, M., et al., 2015. Chimpanzees (Pan troglodytes) produce the same types of 'laugh faces' when they emit laughter and when they are silent. PLoS ONE 10 (6), e0127337.

Davila-Ross, M., Palagi, E., 1863. Laughter, play faces and mimicry in animals: evolution and social functions. Philos. Trans. R. Soc. B: Biol. Sci. 2022 (377), 20210177.

Dawson, L.C., et al., 2019. Humans can identify cats' affective states from subtle facial expressions. Anim. Welf. 28 (4), 519–531.

Defensor, E.B., et al., 2012. Facial expressions of mice in aggressive and fearful contexts. Physiol. Behav. 107 (5), 680–685.

Dickman, C.R., 1996. Impact of exotic generalist predators on the native fauna of Australia. Wildl. Biol. 2 (3), 185–195.

Diogo, R., et al., 2009. On the origin, homologies and evolution of primate facial muscles, with a particular focus on hominoids and a suggested unifying nomenclature for the facial muscles of the Mammalia. J. Anat. 215 (3), 300–319.

Driscoll, C., et al., 2011. A suite of genetic markers useful in assessing wildcat (Felis silvestris ssp.)— domestic cat (Felis silvestris catus) admixture. J. Hered. 102 (Suppl_1), S87–S90.

Ekman, P., Rosenberg, E.L., 2005. What the Face Reveals: Basic and Applied Studies of Spontaneous Expression Using the Facial Action Coding System (FACS). Oxford University Press, New York: New York.

Ekman, P., Rosenberg, E.L., 2005b. What the Face Reveals: Basic and Applied Studies of Spontaneous Expression Using the Facial Action Coding System (FACS), second ed. Oxford University Press, New York, NY, US, p. 639.

Elzerman, A.L., et al., 2020. Conflict and affiliative behavior frequency between cats in multi-cat households: a survey-based study. J. Feline Med. Surg. 22 (8), 705–717.

Evangelista, M.C., et al., 2019. Facial expressions of pain in cats: the development and validation of a feline grimace scale. Sci. Rep. 9 (1), 19128.

Fedurek, P., et al., 2015. Chimpanzee lip-smacking facilitates cooperative behaviour. Sci. Rep. 5 (1), 13460.

Feighelstein, M., et al., 2022. Automated recognition of pain in cats. Sci. Rep. 12 (1), 9575.

Florkiewicz, B., Campbell, M., 2021a. Chimpanzee facial gestures and the implications for the evolution of language. PeerJ 9, e12237.

Florkiewicz, B., Skollar, G., Reichard, U.H., 2018. Facial expressions and pair bonds in hylobatids. Am. J. Phys. Anthropol. 167 (1), 108–123.

Florkiewicz, B.N., Campbell, M.W., 2021b. A comparison of focal and opportunistic sampling methods when studying chimpanzee facial and gestural communication. Folia Primatol. 92 (3), 164–174.

Florkiewicz, B.N.O., Oña, L.S., Campbell, L., M. W, 2023. Primate socio-ecology shapes the evolution of distinctive facial repertoires. J. Comp. Psychol.

Freeberg, T.M., Krams, I., 2015. Does social complexity link vocal complexity and cooperation? J. Ornithol. 156 (1), 125–132.

Gallo, A., et al., 2022. The face never lies: facial expressions and mimicry modulate playful interactions in wild geladas. Behav. Ecol. Sociobiol. 76 (1), 19.

Gouveia, K., Magalhães, A., de Sousa, L., 2011. The behaviour of domestic cats in a shelter: Residence time, density and sex ratio. Appl. Anim. Behav. Sci. 130 (1), 53–59.

Higashiyama, H., et al., 2021. Mammalian face as an evolutionary novelty. Proc. Natl. Acad. Sci. 118 (44), e2111876118.

Julle-Danière, É., et al., 2015. MaqFACS (macaque facial action coding system) can be used to document facial movements in Barbary macaques (Macaca sylvanus). PeerJ 3.

Kaiser, S., Hennessy, M.B., Sachser, N., 2015. Domestication affects the structure, development and stability of biobehavioural profiles. Front Zool. 12 (Suppl 1), S19.

Kaminski, J., et al., 2019. Evolution of facial muscle anatomy in dogs. Proc. Natl. Acad. Sci. 116 (29), 14677–14681.

Kessler, M.R., Turner, D.C., 1999. Socialization and stress in cats (felis silves tris catvs) housed singly and in groups in animal shelters. Anim. Welf. 8 (1), 15–26.

Khoddami, S., Kiser, M.C., Moody, C.M., 2023. Why can't we be friends? Exploring factors associated with cat owners' perceptions of the cat-cat relationship in two-cat households. Front. Vet. Sci. 10.

Kiley-Worthington, M., 1976. The tail movements of ungulates, canids and felids with particular reference to their causation and function as displays. Behaviour 56 (1–2), 69–114.

Kortekaas, K., Kotrschal, K., 2019. Does socio-ecology drive differences in alertness between wolves and dogs when resting? Behav. Process. 166, 103877.

Larkin, M., Radich, R., 2021. Pet population still on the rise, with fewer pets per household. J. Am. Vet. Med Assoc. 259 (11), 1243–1245.

Lausberg, H., Sloetjes, H., 2009. Coding gestural behavior with the NEUROGES-ELAN system. Behav. Res. Methods 41 (3), 841–849.

Leyhausen, P., 1979. Cat Behavior: The Predatory and Social Behavior of Domestic and Wild Cats. Garland STPM Press, New York City, New York.

Liberg, O., et al., 2000. Density spatial organisation and reproductive tactics in the domestic cat and other felids. Incollection 119–148.

Liebal, K., Pika, S., Tomasello, M., 2004. Social communication in siamangs (Symphalangus syndactylus): use of gestures and facial expressions. Primates 45 (1), 41–57.

Llamazares-Martín, C., et al., 2017. Relaxed open mouth reciprocity favours playful contacts in South American sea lions (Otaria flavescens). Behav. Process. 140, 87–95.

Loberg, J.M., Lundmark, F., 2016. The effect of space on behaviour in large groups of domestic cats kept indoors. Appl. Anim. Behav. Sci. 182, 23–29.

Maestripieri, D., Wallen, K., 1997. Affiliative and submissive communication in rhesus macaques. Primates 38 (2), 127–138.

Maglieri, V., et al., 2020. Levelling playing field: synchronization and rapid facial mimicry in dog-horse play. Behav. Process. 174, 104104.

Maglieri, V., et al., 2022. The relaxed open mouth is a true signal in dogs: demonstrating Tinbergen's ritualization process. Anim. Behav. 188, 65–74.

Mancini, G., Ferrari, P.F., Palagi, E., 2013. In play we trust. Rapid facial mimicry predicts the duration of playful interactions in geladas. PLoS ONE 8 (6), e66481.

Mathôt, S., 2018. Pupillometry: psychology, physiology, and function. J. Cogn. 1 (1), 16.

Montague, M.J., et al., 2014. Comparative analysis of the domestic cat genome reveals genetic signatures underlying feline biology and domestication. Proc. Natl. Acad. Sci. USA 111 (48), 17230–17235.

Natoli, E., Baggio, A., Pontier, D., 2001. Male and female agonistic and affiliative relationships in a social group of farm cats (Felis catus L.). Behav. Process. 53 (1–2), 137–143.

No authorship, i., Guidelines for the treatment of animals in behavioural research and teaching. Animal Behaviour, 2020. 159: p. i-xi.

Oña, L.S., Sandler, W., Liebal, K., 2019. A stepping stone to compositionality in chimpanzee communication. PeerJ 7, e7623.

Palagi, E., 2008. Sharing the motivation to play: the use of signals in adult bonobos. Anim. Behav. 75 (3), 887–896.

Palagi, E., et al., 2019a. Sharing playful mood: rapid facial mimicry in Suricata suricatta. Anim. Cogn. 22 (5), 719–732.

Palagi, E., et al., 2019b. Facial mimicry and play: a comparative study in chimpanzees and gorillas. Am. Psychol. Assoc.: US 665–681.

Palagi, E., Mancini, G., 2011. Playing with the face: playful facial "chattering" and signal modulation in a monkey species (Theropithecus gelada). J. Comp. Psychol. 125 (1), 11.

Palagi, E., Norscia, I., Spada, G., 2014. Relaxed open mouth as a playful signal in wild ring-tailed lemurs. Am. J. Prima 76 (11), 1074–1083.

Palagi, E., Nicotra, V., Cordoni, G., 2015. Rapid mimicry and emotional contagion in domestic dogs. R. Soc. Open Sci. 2 (12), 150505.

Parker, H.G., Shearin, A.L., Ostrander, E.A., 2010. Man's best friend becomes biology's best in show: genome analyses in the domestic dog. Annu. Rev. Genet. 44, 309–336.

Parr, L.A., et al., 2007. Classifying chimpanzee facial expressions using muscle action. Emot. (Wash., D. C.) 7 (1), 172–181.

Parr, L.A., et al., 2010. Brief communication: MaqFACS: a muscle-based facial movement coding system for the rhesus macaque. Am. J. Phys. Anthropol. 143 (4), 625–630.

Parr, L.A., Cohen, M., Waal, Fd, 2005. Influence of social context on the use of blended and graded facial displays in chimpanzees. Int. J. Primatol. 26 (1), 73–103.

Penar, W., Klocek, C., 2018. Aggressive behaviors in domestic cats (Felis catus). Ann. Wars. Univ. Life Sci. SGGW Land Reclam. 52, 143–150.

Pika, S., Fröhlich, M., 2019. Gestural acquisition in great apes: the social negotiation hypothesis. Anim. Cogn. 22 (4), 551–565.

Preuschoft, S., van Hooff, J.M., 1997. The Social Function of "Smile" and "Laughter": Variations Across Primate Species and Societies. Lawrence Erlbaum Associates, Inc.

Range, F., Marshall-Pescini, S., 2022. Domestication Hypotheses Relating to Behaviour and Cognition: Which Are Supported by the Current Data? In: Range, F., Marshall-Pescini, S. (Eds.), Wolves and dogs: between myth and science. Springer International Publishing, Cham, pp. 335–373.

Reid, J., Nolan, A., Scott, E., 2018. Measuring pain in dogs and cats using structured behavioural observation. Vet. J. 236, 72–79.

Ross, K.M., Bard, K.A., Matsuzawa, T., 2014. Playful expressions of one-year-old chimpanzee infants in social and solitary play contexts. Front. Psychol. 5.

Santana, S.E., Dobson, S.D., Diogo, R., 2014. Plain faces are more expressive: comparative study of facial colour, mobility and musculature in primates. Biol. Lett. 10 (5), 20140275.

Scheider, L., et al., 2014. A comparison of facial expression properties in five hylobatid species. Am. J. Primatol. 76 (7), 618–628.

Scheider, L., et al., 2016. Social use of facial expressions in hylobatids. PLoS ONE 11 (3), e0151733.

Schilder, M.B.H., et al., 1984. A quantitative analysis of facial expression in the plains zebra. Z. für Tierpsychol. 66 (1), 11–32.

Scopa, C., Palagi, E., 2016. Mimic me while playing! Social tolerance and rapid facial mimicry in macaques (Macaca tonkeana and Macaca fuscata). J. Comp. Psychol. 130 (2), 153–161.

Smith, M.J., Harper, D.G.C., 1995. Animal signals: models and terminology. J. Theor. Biol. 177 (3), 305–311.

Steagall, P.V., Monteiro, B.P., 2019. Acute pain in cats: Recent advances in clinical assessment. J. Feline Med. Surg. 21 (1), 25–34.

Stelow, E.A., Bain, M.J., Kass, P.H., 2016. The relationship between coat color and aggressive behaviors in the domestic cat. J. Appl. Anim. Welf. Sci. 19 (1), 1–15.

Taylor, D., et al., 2019. Facial complexity in sun bears: exact facial mimicry and social sensitivity. Sci. Rep. 9 (1), 4961.

Team, R.C, R: A language and environment for statistical computing. R Foundation for Statistical Computing. 2021: Vienna, Austria.

Tomasello, M., Call, J., 2019. Thirty years of great ape gestures. Anim. Cogn. 22 (4), 461–469.

Travnik, Id.C., et al., 2020. Temperament in domestic cats: a review of proximate mechanisms, methods of assessment, its effects on human—cat relationships, and one welfare. Animals 10 (9), 1516.

Turner, D.C., 2017. A review of over three decades of research on cat-human and human-cat interactions and relationships. Behav. Process. 141, 297–304.

Usui, K., Tokita, M., 2018. Creating diversity in mammalian facial morphology: a review of potential developmental mechanisms. EvoDevo 9 (1), 15.

van de Waal, E., et al., 2013. Negotiations over grooming in wild vervet monkeys (Chlorocebus pygerythrus). Int. J. Primatol. 34 (6), 1153–1171.

Vick, S.-J., et al., 2007. A cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). J. Nonverbal Behav. 31 (1), 1–20.

Vitale, K., 2022b. Normal feline social behavior. Clin. Handb. Feline Behav. Med. 10–21.

Vitale, K.R., 2022a. The social lives of free-ranging cats. Anim. (Basel) 12 (1).

Wagner, D., Hurley, K., Stavisky, J., 2018. Shelter housing for cats: practical aspects of design and construction, and adaptation of existing accommodation. J. Feline Med. Surg. 20 (7), 643–652.

Waller, B.M., et al., 2012. GibbonFACS: a muscle-based facial movement coding system for hylobatids. Int. J. Primatol. 33 (4), 809–821.

Waller, B.M., et al., 2013a. Pseudoreplication: a widespread problem in primate communication research. Anim. Behav. 86 (2), 483–488.

Waller, B.M., et al., 2013a. Paedomorphic facial expressions give dogs a selective advantage. PLoS ONE 8 (12), e82686.

Waller, B.M., Dunbar, R.I.M., 2005. Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (Pan troglodytes). Ethology 111 (2), 129–142.

Waller, B.M., Micheletta, J., 2013. Facial expression in nonhuman animals. Emot. Rev. 5 (1), 54–59.

Waller, B.M., Caeiro, C.C., Davila-Ross, M., 2015. Orangutans modify facial displays depending on recipient attention. PeerJ 3.

Waller, B.M., Whitehouse, J., Micheletta, J., 2016. Macaques can predict social outcomes from facial expressions. Anim. Cogn. 19 (5), 1031–1036.

Waller, B.M., Whitehouse, J., Micheletta, J., 2017. Rethinking primate facial expression: a predictive framework. Neurosci. Biobehav. Rev. 82, 13–21.

Waller, B.M., Julle-Daniere, E., Micheletta, J., 2020. Measuring the evolution of facial 'expression' using multi-species FACS. Neurosci. Biobehav. Rev. 113, 1–11.

Waller, B., et al., 2013b. DogFACS: the dog facial action coding system.

Wathan, J., et al., 2015. EquiFACS: the equine facial action coding system. PLOS ONE 10 (8), e0131738.

Yamaguchi, N., et al., 2004. Craniological differentiation between European wildcats (Felis silvestris silvestris), African wildcats (F. s. lybica) and Asian wildcats (F. s. ornata): implications for their evolution and conservation. Biol. J. Linn. Soc. 83 (1), 47–63.

Yeon, S.C., et al., 2011. Differences between vocalization evoked by social stimuli in feral cats and house cats. Behav. Process. 87 (2), 183–189.

Yu, H., et al., 2021. Genomic evidence for the Chinese mountain cat as a wildcat conspecific (Felis silvestris bieti) and its introgression to domestic cats. Sci. Adv. 7 (26), eabg0221.

Zhang, Y.J., et al., 2019. Social functions of relaxed open-mouth display in golden snub-nosed monkeys (Rhinopithecus roxellana). Zool. Res 40 (2), 113–120.