

University of Helsinki  
Dissertationes Universitatis Helsingiensis 173/2024

Department of Veterinary Bioscience, Faculty of Veterinary Medicine  
University of Helsinki  
Folkhälsan Research Center

# **Feline personality and problematic behaviour**

*Associations with demographic, genetic, and environmental factors*

Salla Mikkola

ACADEMIC DISSERTATION

To be presented for public discussion with the permission of the Faculty of  
Veterinary Medicine of the University of Helsinki, in Hall I, Biomedicum, on the  
23rd of August 2024 at 15 o'clock.

Helsinki 2024

**Supervisors**

Professor Hannes Lohi, PhD  
University of Helsinki  
Folkhälsan Research Center  
Helsinki, Finland  
Docent Anna-Maija Virtala, PhD, MSc, DVM  
University of Helsinki  
Helsinki, Finland  
Postdoctoral Researcher Milla Salonen, PhD  
University of Helsinki  
Folkhälsan Research Center  
Helsinki, Finland  
University of Turku  
Turku, Finland

**Reviewers**

Docent Sonja Koski, PhD  
University of Helsinki  
Helsinki, Finland  
University of Turku  
Turku, Finland  
Associate Professor Lee Niel, PhD  
University of Guelph  
Guelph, Ontario, Canada

**Opponent**

Assistant Professor Kristyn Vitale, PhD  
Unity Environmental University  
New Gloucester, Maine, United States

Cover photographs: Stock.adobe.com & Shutterstock.com

Publisher: Helsingin yliopisto

Series: Dissertationes Universitatis Helsingiensis 173/2024

ISBN 978-951-51-9910-2 (print)

ISBN 978-951-51-9909-6 (online)

ISSN 2954-2898 (print)

ISSN 2954-2952 (online)

PunaMusta

Joensuu 2024

*The Faculty of Veterinary Medicine uses the Urkund system (plagiarism recognition) to examine all doctoral dissertations.*



# Abstract

Behaviour is a familiar, yet complex subject to understand as it is affected by several factors, such as genes or environment, and their interactions. Behaviour and personality, the stable behavioural differences between individuals, have an essential role in evolution, as they can affect the adaptation of an individual to their environment. In the case of pet animals, the behaviour can sometimes be problematic for its owner, the animal itself, or both.

The domestic cat is the most popular pet animal. However, the popularity is shadowed by problematic behaviours, which can decrease the welfare of both the owner and the cat. As a common and recognised issue, problematic behaviour has interested researchers, who have found several, but often inconsistent risk factors for the problems. Moreover, previous studies have usually lacked validation and the number of acknowledged background factors has been limited.

The aims of this thesis are to investigate the structure of feline personality and factors associated with common problematic behaviours in cats. The targeted problematic behaviours were fearfulness, aggression toward humans, excessive grooming, and litterbox issues. The data were collected with an owner-completed online survey that was tested for validity and reliability. In addition to personality and behaviour, information about the cats' background and health was collected.

The datasets consisted of 3036–4316 cats from 26 breed/breed groups, depending on the study. The datasets were analysed with different methods, including explanatory factor analysis for the structure of personality and behaviour, and generalized linear models with model selection for the risk factors of problematic behaviours. Validity and reliability were examined, e.g., with inter-rater and test-retest estimates, and the importance of the found factors was estimated with relative and absolute effect sizes.

The results of this thesis show that problematic behaviours are complex and affected by various factors, which explain only a small proportion of the variance in the behaviours. Nevertheless, the breed and personality, especially fearfulness and sociability, were among the most important factors associated with the studied behaviours. Fearfulness was related to all other problematic behaviours, possibly indicating that it is genetically or neurologically interconnected with them. Sociability toward cats was associated with decreased aggression and house soiling, and sociability toward humans was likewise associated with decreased fearfulness and aggression but increased excessive grooming.

Some of the identified factors replicate previous studies, but we also revealed new associations. The findings may have a preventive effect, e.g., the proper socialization of kittens may decrease fearfulness and other problems linked to it. The findings may also help to solve current problems, e.g., by modifying the identified risk factors in the current living environment.

# Tiivistelmä

Käyttäytyminen on arkipäiväinen, mutta monimutkainen ilmiö, jota ohjaavat useat geenit, ympäristötekijät sekä näiden keskinäiset vuorovaikutukset. Käyttäytymisellä ja persoonallisuudella, pysyvillä yksilöiden välisillä eroilla käyttäytymisessä, on tärkeä rooli evoluutiossa sillä ne vaikuttavat yksilön sopeutumiseen ympäristöönsä. Erityisesti seuraeläimillä esiintyy myös omistajille, eläimille tai molemmille ongelmallisia käyttäytymispiirteitä.

Kissat ovat suosittuja seuraeläimiä, mutta myös niillä esiintyy ongelmallista käyttäytymistä, joka voi vaikuttaa sekä omistajan että kissan hyvinvointiin. Yleisenä haasteena ongelmallinen käyttäytyminen on herättänyt tutkijoiden mielenkiinnon ja ongelmille on löydetty useita, mutta keskenään usein ristiriitaisia selittäviä tekijöitä. Aikaisempien tutkimuksen luotettavuutta ei ole yleensä myöskään mitattu ja mukaan otettujen taustatekijöiden valikoima on ollut rajallinen.

Tämän väitöskirjatyön tavoitteina oli tutkia kissojen persoonallisuuden rakennetta ja kissojen yleisiin ongelmallisiin käyttäytymispiirteisiin vaikuttavia tekijöitä. Tutkitut käyttäytymispiirteet olivat pelokkuus, ihmisiin kohdistuva aggressiivisuus, itsensä pakonomainen peseminen ja sisäsiisteysongelmat. Tutkimusaineisto kerättiin kissojen omistajille suunnatulla internet-kyselyllä, jonka luotettavuus testattiin. Persoonallisuuden ja käyttäytymisen lisäksi aineistoa kerättiin myös kissan taustasta ja terveydestä.

Aineiston koko vaihteli osatutkimuksien välillä 3036 kissasta 4316 kissaan, 26 eri rotu/roturyhmästä. Aineisto analysoitiin käyttäen erilaisia menetelmiä, kuten faktorianalyysiä persoonallisuuden ja käyttäytymisen rakenteen selvittämisessä sekä yleistettyjä lineaarisia malleja ongelmallisiin piirteisiin vaikuttavien tekijöiden tunnistamisessa. Luotettavuutta mitattiin muun muassa vastaajien kesken ja vastauksetojen välillä, jonka lisäksi arviotiin löydettyjen tekijöiden suhteellista ja absoluuttista tärkeyttä.

Väitöskirjatyön tulokset vahvistavat ongelmallisten käyttäytymispiirteiden olevan monimutkaisia ja niihin vaikuttavan useat eri tekijät, jotka yksinään selittävät kuitenkin vain pienen osan käyttäytymisen vaihtelusta. Tärkeimmiksi tekijöiksi nousivat kissan rotu ja persoonallisuus, erityisesti pelokkuus ja sosiaalisuus. Pelokkuus yhdistyi jokaiseen ongelmalliseen käyttäytymispiirteeseen, mikä voi viitata yhteiseen hermostolliseen tai geneettiseen taustaan. Sosiaalisuus toisia kissoja kohtaan yhdistyi vähentyneeseen aggressiivisuuteen ja sisäsiisteysongelmiin, ja sosiaalisuus ihmisiä kohtaan vähentyneeseen pelokkuuteen ja aggressiivisuuteen, mutta lisääntyneeseen pakonomaiseen pesemiseen.

Osa tekijöistä oli löydetty jo aiemmin, osa yhteyksistä oli täysin uusia. Väitöskirjatyön tuloksia voidaan hyödyntää ongelmien ehkäisyssä, kuten kissanpentujen riittävää sosiaalistamista pelokkuuden ennaltaehkäisyssä. Tuloksen voivat auttaa myös ongelmallisen käyttäytymisen hoidossa nyky-ympäristön muokkaamisen avulla.

# Contents

Abstract .....	1
Tiivistelmä.....	2
List of original publications .....	5
Author’s contribution.....	6
Abbreviations .....	7
1 Introduction .....	8
2 Review of the literature.....	9
2.1 Behaviour and personality .....	9
2.1.1 Factors influencing behaviour.....	10
2.1.2 Measuring behaviour.....	12
2.2 The study species: the domestic cat .....	12
2.3 Feline behaviour & personality .....	15
2.3.1 Factors associating with feline personality & behaviour .....	18
2.4 Problematic behaviour .....	21
2.4.1 Common problematic behaviours in cats .....	22
3 Aims of the study.....	25
4 Materials and methods.....	26
4.1 Ethical statement.....	26
4.2 The survey and data collection.....	26
4.3 Subjects.....	28
4.4 Construction of explanatory variables .....	28
4.5 Statistical analyses.....	30
4.5.1 Personality and behaviour structure, validity, reliability, and breed differences (study I) .....	30

4.5.2	Model selection of fearfulness, aggression toward humans, and excessive grooming (study II) .....	31
4.5.3	Model selection of house soiling and litter box fussiness models (study III) .....	32
4.5.4	Model fit and extraction of the results (studies II & III) .....	33
4.5.5	Importance of the variables (studies II & III) .....	34
5	Results .....	35
5.1	Behaviour and personality structure, reliability, and validity .....	35
5.2	Factors associated with problematic behaviours .....	39
5.2.1	Personality and behaviour correlates .....	40
5.2.2	Environmental factors of behaviour .....	41
5.2.2.1	Early life conditions .....	41
5.2.2.2	Current environment & environmental enrichment .....	41
5.2.2.3	Owner & health-related factors .....	43
5.2.3	Demographic factors of behaviour .....	43
5.2.4	Breed differences .....	45
5.2.5	Importance of the variables .....	47
6	Discussion .....	50
6.1	The structure of feline personality and behaviour .....	52
6.2	Reliability and validity of the survey .....	53
6.3	Factors associating with problematic behaviours .....	55
6.3.1	Personality and behaviour traits & problematic behaviour .....	55
6.3.2	Early life socialization & other environmental factors contribute to problematic behaviour .....	56
6.3.3	Breeds differ in their behaviour & personality .....	60
6.4	Importance of factors .....	62
7	Conclusions .....	64
	Acknowledgements .....	67
	References .....	69

# List of original publications

This thesis is based on the following publications:

- I Mikkola, S., Salonen, M., Hakanen, E., Sulkama, S., and Lohi, H. (2021). Reliability and validity of seven feline behaviour and personality traits. *Animals* 11, 1991.
- II Mikkola, S., Salonen, M., Hakanen, E., and Lohi, H. (2022). Fearfulness associates with problematic behaviours and poor socialization in cats. *iScience* 25, 105265.
- III Mikkola, S., Salonen, M., Hakanen, E., and Lohi, H. (2023). Feline litter box issues associate with cat personality, breed, and age at sterilization. *JAVMA*, 1–9.

The publications are referred to in the text by their roman numerals.

# Author's contribution

Author's contribution to each publication:

## **I Reliability and validity of seven feline behaviour and personality traits**

The author participated in the study design and data collection, conducted the statistical analyses with the help of M. Salonen, and wrote the manuscript with help from coauthors. The author planned the figures with coauthors and the figures were created by M. Salonen and the author.

## **II Fearfulness associates with problematic behaviours and poor socialization in cats**

The author participated in the study design and data collection, conducted the statistical analyses with the help of M. Salonen, and wrote the manuscript with help from coauthors. The author planned the figures with coauthors and the figures were created by M. Salonen and the author.

## **III Feline litter box issues associate with cat personality, breed, and age at sterilization**

The author participated in the study design and data collection, conducted the statistical analyses with the help of M. Salonen, and wrote the manuscript with help from coauthors. The author planned the figures with coauthors and the figures were created by M. Salonen and the author.

# Abbreviations

AIC	Akaike Information Criterion
ARB	abnormal repetitive behaviour
EFA	explanatory factor analysis
e.g.	exempli gratia
FDR	false discovery rate
GLM	generalized linear model
ICC	intraclass correlation coefficient
i.e.	id est

# 1 Introduction

The domestic cat is a popular pet, but their personality and behaviour have remained less studied than another popular pet animal, the domestic dog. The living conditions of the pet cats differ greatly from their ancestor, the solitary African wildcat, by usually limited living space and social environment. During domestication, behaviour of the cat was remarkably changed, and it became a more social species. The behaviour and personality, stable behavioural differences between individuals, are affected at least by numerous genes, the environment, and their complex interactions. The structure of personality and behaviour have been studied, for example, with surveys, which, however, usually lack the investigation of validity and reliability.

Although the cat's behaviour shows great plasticity, problematic behaviour may occur in unideal living conditions or for other, partly unidentified reasons. Problematic behaviours are usually, but not always, based on normal behaviour that has become excessive. The most common problems in cats are fearfulness, aggressiveness, and house soiling. In addition, like other animals, cats can have abnormal repetitive behaviours (ARBs), such as pica (the consumption of non-food items) and excessive grooming. Problematic behaviour can cause diverse problems both to the cat and its owner, as it can be harmful to the cat, and it usually weakens the cat-owner bond. The most severe cases can lead to the relinquishment or euthanasia of the cat. Previous literature has reported several potential risk factors, but the results of the studies have been contradictory.

This thesis hypothesises that the cats' behaviours show stable differences between individuals, thus forming their personality consisting of different traits. Moreover, the thesis hypothesises that the studied problematic behaviours, fearfulness, aggression toward humans, excessive grooming, and litterbox issues are affected by several factors. Therefore, this thesis investigates the association of personality, demographics, environment, and genetic background with problematic behaviours. The findings stress the complexity of problematic behaviour and behaviour in general, as several associations were found. The results highlight the importance of personality traits, especially fearfulness, in the occurrence of problematic behaviour. Managing the associated risk factors in the cats' rearing and current environments may reduce problematic behaviour, possibly improving the welfare both cats and their owners.

## 2 Review of the literature

### 2.1 Behaviour and personality

Behaviour is usually described as the internally coordinated responses (actions or inactions) of a whole living organism to internal and/or external stimuli, excluding responses arising from developmental changes, although there are different definitions for the term even between behaviour researchers (Levitis et al., 2009). Thus, the animal can behave by acting (for example, flee a predator) or becoming inactive (for example, freeze when detecting a predator). In addition, the stimulus can be external, such as a hunting attempt toward a prey animal when seeing one, or internal, such as hunger or thirst. Behaviour, as defined here, can be found throughout the animal kingdom and even plants and unicellular organisms (Levitis et al., 2009).

Personality is usually described as behavioural traits that are relatively stable over time and across different contexts (Carere & Maestriperi, 2013). Synonyms used to describe the same phenomenon as the personality in the previous literature are behavioural syndromes, coping styles, and temperament (Carere & Maestriperi, 2013). The personality traits form together the personality of an individual. Together the traits form the structure of personality, which can be studied, for example, at the species level.

Personality was first studied only in humans (*Homo sapiens sapiens*), as it was previously thought that humans are the only species capable of having personalities (Gosling, 2008). However, later the stable behavioural differences between individuals, i.e., personalities, have been found widely among different animal species from other primates (King & Figueredo, 1997) to cats (Travnik et al., 2020), dogs (Gosling et al., 2003), and even invertebrates, such as anemones (Briffa & Greenaway, 2011).

Researchers have suggested several different traits and structures forming the basis of personality. Aggressiveness, activity, shyness/boldness, fearfulness, reactivity, and sociability are commonly found traits in wild animals (Gartland et al., 2022; Sih et al., 2004). In domesticated animals, sociability toward humans is also a commonly found trait (e.g. Udell et al., 2010; Vitale & Udell, 2019). Especially in pet animals, such as dogs and cats, sociability toward humans is an important trait, as more sociable animals adapt more easily to human-based environments (Shin & Shin, 2017) and people tend to prefer sociable individuals

(Turner, 2021). Behavioural differences between populations and individuals play an important role in evolutionary ecology as well, as they potentially affect, for example, birth, death, and dispersal rates of wild animals (Sih et al., 2004; Wolf & Weissing, 2012).

Behaviour can also be harmful to the individual itself if it disturbs its daily functioning, such as eating, and may therefore affect the survival of the individual. In humans, behaviour like this can be classified as a psychiatric disorder; in non-human animals, the term behavioural problem is (usually) used instead. This kind of behaviour is mostly documented in animals in captivity, especially fear-related problems are prevalent. Another, although much rarer, type of harmful behaviour is abnormal repetitive behaviour (ARB) (Garner, 2005; Tynes & Sinn, 2014). Comorbidity of behavioural problems are common (Goldstein-Piekarski et al., 2016; Salonen et al., 2020) and previous findings have shown that they are more prevalent with specific personalities (Dinwoodie et al., 2019). Thus, it is suggested that individuals with specific personality traits are more prone to developing behavioural problems.

### **2.1.1 Factors influencing behaviour**

The behaviour is modified by genes and the environment, and their complex interactions (Overall et al., 2014). The genetics of an individual provides the framework for the other factors influencing the behaviour. If an individual (i.e., genotype) is transferred to a different environment, its phenotype can change as well. This phenomenon is called phenotypic plasticity or genotype-by-environment interaction (GxE), and it differs between individuals (Kelly et al., 2012). It also appears to be heritable (Kelly et al., 2012). The changes in the phenotypes can be developmental, such as growing muscle mass because of exercising, or behavioural, such as fearful behaviour among strangers.

Genetics are an important component in behaviour, although the effect of an individual gene is small (Overall et al., 2014). The contribution of genetic variation to a phenotype can be measured with heritability estimates (Dochtermann et al., 2019). As heritability is the proportion of total phenotypic variance that is attributable to additive genetic variance, it varies between 0 and 1. A high estimate (closer to 1) means that the majority of the phenotypic variation is explained by genetic differences between individuals (Dochtermann et al., 2019). According to the newest meta-analysis, in non-human animals, the average heritability of behaviour is 0.235 (Dochtermann et al., 2019) and the average heritability of personality is 0.52 (Dochtermann et al., 2015), which means that genetic variation explains a remarkable proportion of overall phenotypic variation, especially of personality. However, the estimates vary greatly between traits, studies, and animal populations (van Oers & Sinn, 2013). Similarly, psychiatric disorders and behavioural problems may have genetic components that are somewhat heritable.

In addition, epigenetics, the biochemical mechanisms that alter gene expression without changing the primary nucleotide sequence of the genome, have been shown to affect individual's phenotype and to be heritable (Richards, 2006).

Hormones can also alter behaviour (Bernstein et al., 1983). For example, the gut microbiota-brain axis is an interesting network where the gut microbiota modulates the behaviour of its animal host through chemical communication with the nervous system (Morais et al., 2021). The details of this pathway are still poorly understood, but previous studies have found a link between the composition of the microbiota and neurodegenerative disorders, stress, depression, and anxiety (Morais et al., 2021).

There is no doubt that the environment plays a big role in behaviour. However, a given environmental factor does not necessarily affect different individuals in the same way due to genotypic plasticity. An individual is affected by the environment even before it is born; for example, maternal stress increases the probability of anxiety and learning problems both in humans and non-human animals (McLean et al., 2019; Weinstock, 2008). The early life period, here meaning the time before maturation or weaning, is a particularly important time for the development of the behaviour. Stress during this time has negative impacts on mental and physical health in humans as well as in non-human animals (Salonen, 2020). For example, poor quality of maternal care, early weaning, or absence of the mother increases anxiety-like behaviours, as well as aggressive and abnormal repetitive behaviours (e.g., (Ahola et al., 2017; Tiira & Lohi, 2015)).

The current social and physical environment affect the behaviour of the individual as well. Many animal species are capable of social learning, i.e., learning by observing or interacting with other individuals (Galef & Laland, 2005), and in some species, such as apes, this has led to cultural evolution (Whiten, 2019). The possibility to interact with conspecifics seems to be important for pet animals as well, as the company of other animals is associated to lower aggressiveness and fearfulness (Amat et al., 2009; Hsu & Sun, 2010; Tiira & Lohi, 2015; Yamada et al., 2020). For domesticated animals, the environment should be stimulating enough that one can display normal behaviours, but not too unpredictable, as it can trigger problematic behaviours (Amat et al., 2016).

In addition, demographic factors may affect behaviour. For example, personality usually changes during ageing. Humans tend to be more neurotic at young age (Bleidorn et al., 2022; Ståhl et al., 2023), and companion animals more active and playful, but less aggressive (Duffy et al., 2017; Gartner, 2015; Hsu & Sun, 2010; Yamada et al., 2020). Sex and hormonal status likely have their own contribution to behaviour (e.g., (Amat et al., 2009; Hsu & Sun, 2010; Mikkola, Salonen, Puurunen, et al., 2021; Weldon et al., 2010)), but the findings differ greatly between the studies (Mikkola, Salonen, Puurunen, et al., 2021).

To sum up, various genetic, environmental, and other factors alter the behaviour of an individual. As these factors interact also with each other the effects are complicated and some remain undiscovered.

### **2.1.2 Measuring behaviour**

Measuring behaviour is challenging for several reasons: it has a temporal component, several behaviours can coexist at the same time, it can be affected by unidentified factors, and it varies between and within individuals (Bateson & Martin, 2021). Behaviour has been studied with multiple different methods, including naturalistic observations, test batteries, and surveys (Freeman et al., 2011). In companion animals, the latter two methods are the most common.

Test batteries, such as behavioural tests, are standardized tests that can be used to target specific behaviours. However, they capture only a limited moment of the subject's behaviour, compared to surveys, which measure the behaviour from a longer time period. In animal studies, the owner or caretaker of the animal is usually the one completing the survey. Thus, questionnaires can be more subjective in nature than direct coding methods. However, with surveys, it is easier and less time-consuming to collect large datasets than with behaviour testing. In addition, they are usually less problematic ethically than experimental studies (Bateson & Martin, 2021). Due to the different strengths and weaknesses of different methodologies, it is recommended to measure the behaviour with more than one approach (Bateson & Martin, 2021).

The quality of behavioural studies can greatly vary; thus, it is important to estimate both the reliability and validity of the behavioural measurements (Bateson & Martin, 2021). Reliability measures how well the measurements are repeatable and the validity whether the right quality is being measured (Bateson & Martin, 2021). Validity can be assessed by comparing the results with previously published studies about the same phenomenon, preferably with an existing gold standard (Bateson & Martin, 2021), or by comparing the results of a survey with behaviour tests or vice versa. Test-retest reliability and inter-rater reliability measures are common reliability estimators. Test-retest reliability evaluates the repeatability of measurement within the observer and inter-rater reliability between the observers. Despite the selected methodology, estimating the reliability is important as a major source of inaccuracy in behavioural measurements comes from human observers (Bateson & Martin, 2021).

## **2.2 The study species: the domestic cat**

The domestication of the cat (*Felis catus* Linnaeus, 1758) took place ~ 12 000 years ago somewhere in the Near East, overlapping the development of agriculture in the Fertile Crescent (Nilson et al., 2022; Ottoni et al., 2017). The domestication

process from the wild African wildcat (*Felis silvestris lybica* Forster, 1780) was likely a natural and commensalistic process (Ottoni et al., 2017). The African wildcat is a small, obligate carnivore, which preys on small animals, such as rodents. Thus, the grain stores likely attracted small rodents, which themselves attracted the wildcats close to the human settlements (Driscoll et al., 2009; Nilson et al., 2022).

From the first places of domestication, the domesticated cats dispersed to the ancient Levant and Egypt (Ottoni et al., 2017), where purposeful breeding of the cat likely started (Kurushima et al., 2012). Cats bred in Egypt were popular among the people and it is suggested that changes in the tameness and human sociability happened during that time (Ottoni et al., 2017). From there, cats dispersed with humans through Eurasia, possibly to control the house mouse (*Mus musculus* Linnaeus, 1758) populations (Krajcarz et al., 2022). To other continents, Australia and the Americas, for example, cats likely dispersed by imperialism, exploration and colonization (Nilson et al., 2022), as they were used to control rodents on sea voyages as well (Ottoni et al., 2017).

During domestication, some morphological changes occurred. Compared to the wildcat, domestic cats are smaller on average (Krajcarz et al., 2022) and they have smaller cranial volumes indicating smaller brains (Lesch et al., 2022). In addition, their facial morphology is somewhat different as domestic cats, on average, have shorter nose lengths than African wildcats (Hattori et al., 2022). This change is likely influenced by humans, as people prefer cats with shorter nose lengths (Hattori et al., 2022).

Modern breeding started in the nineteenth century when certain types of cats were artificially selected from regional, local cat populations (Lipinski et al., 2008). The selection was mainly based on the “visible” aesthetic variation, such as coat colouration, pattern, and length (Nilson et al., 2022; Ottoni & Neer, 2020) (Figure 1), although the local populations differed genetically from each other as well (Lipinski et al., 2008). The group of domestic cats that underwent intensive artificial selection is called the pedigree (purebred) cat, even though the local populations still exist today (Lipinski et al., 2008). In fact, there are more random-bred cats than pedigree cats (Gandolfi & Alhaddad, 2015). The cats originating from local, random-bred populations are sometimes referred to as landrace cats. Finland has its own local “breed”, the Finnish landrace cat.

The first breeds gave a basis to develop new breeds by crossbreeding them with other breeds, with non-pedigree cats that had a visually interesting mutations, or even with other feline species, such as with the Asian leopard cat (*Prionailurus bengalensis* Kerr, 1792) (Lipinski et al., 2008; Martos Martinez-Caja et al., 2021). Intensive breeding has led to several breed-specific health issues, caused by their changed anatomy (Gunn-Moore et al., 2008) and decreased genetic variance, which can be a consequence of, inbreeding and genetic bottlenecks, for example

(Gandolfi & Alhaddad, 2015). Currently, The International Cat Association TICA recognises up to 73 cat breeds (*The International Cat Association, 2018*).



**Figure 1** A) African wildcat with a typical mackerel pattern, B) Colour and pattern variation in a domestic free-ranging cat population, C) Bengal, a hybrid cat breed (*Prionailurus bengalensis* x *Felis catus*), D) Sphynx, a hairless cat breed, E) Persian, a longhaired and brachycephalic cat breed. Photos: stock.adobe.com.

However, the most relevant change during the domestication has happened in the behaviour of the domestic cat. Although the domestic cat and African wildcat still greatly resemble each other genetically, signs of selection have been found in the genomic regions related to behaviour (Montague et al., 2014). Genes located in those regions are related to memory, fear conditioning, and stimulus-reward learning (Montague et al., 2014). As a result, the domestic cats are more tolerant of humans and other animals than the African wildcat. Unlike the solitary African wildcat, the social behaviour of the domestic cat shows great plasticity (Vitale, 2022). They are able to live in restricted spaces among artificial, human-selected groups, and unowned cats can also form colonies themselves in the right circumstances (Natoli et al., 2022). Individuals of the same group can, for example, allogroom each other, defend their territory, play, sleep, and take care of the kittens together (Natoli et al., 2022; Vitale, 2022). On the other hand, some individuals prefer to live alone, and other cats can be a source of stress for them (Vitale, 2022).

To communicate with humans, the domestic cat uses both visual and vocal signals, originating from communication with other cats (Turner, 2021).

Interactions with humans can include, playing, being petted, grooming, and handling, for example (Rochlitz, 2005). Cats can discriminate human attentional state and are able to form deep bonds with their human caregivers (Vitale et al., 2019). The complexity of the cat-human bond parallels any other complex social relationship (Ines et al., 2021). As they can form social relationships with other species, it is suggested that the modern domestic cat is a social generalist (Vitale et al., 2019).

Despite remarkable changes in the behaviour, the domestic cat still has species-specific behavioural needs originating from its wild ancestor including scent marking, crepuscular activity, predatory behaviour, possibility for hiding, and access to elevated places. As the cat is a prey animal as well as a predator, the ability to feel secure is very important to their welfare. Compared to humans, cats have a more sensitive olfactory sense and a wider auditory frequency, thus, aversive odours, such as cleaning chemicals, and loud noises can be stressful for them (J. L. Stella & Buffington, 2016). Additionally, cats prefer a warmer ambient temperature than many other species (J. L. Stella & Buffington, 2016), as their thermoneutral zone is 30–38°C (National Research Council (NRC), 2006). That is remarkably higher than the general ambient room temperature, thus offering beddings that allow cats to thermoregulate themselves are recommended (J. L. Stella & Croney, 2016).

Environmental enrichment, the beneficial modification of the home environment, is usually needed to fulfil cats' behavioural needs, especially with indoor-only cats (Strickler & Shull, 2013). Cats should have, for example, enough space to roam, litterboxes, comfortable resting areas, opportunity to play, scratch, and possibilities for social interaction with their caregiver and other cats (if the cat enjoys the company of conspecifics) (Rochlitz, 2005). Failure to fill one or more of these demands can lead to problematic behaviour (J. L. Stella & Croney, 2016). In addition to species-specific needs, some cats have their own individual-specific needs (Strickler & Shull, 2013), which are often affected by the personality of the individual in question.

## **2.3 Feline behaviour & personality**

Personality and behaviour of the cat is less studied than the personality of the domestic dog, another popular pet animal. However, understanding feline personality and behaviour is important for their welfare, as identifying the cat's personality enables modifying the environment to be more suitable for its individual needs (Foster & Ijichi, 2017; Gartner, 2015). Moreover, owners seem to prefer cats that match their personality type (Zeigler-Hill & Highfill, 2010). As personality has a heritable component, knowing the personality types of individuals used in breeding also benefit cat breeding programs.

The structure of the cat's personality greatly differs between studies; the number of recognised personality dimensions ranges from one to six (Travnik et al., 2020). The most commonly studied traits are related to friendliness, aggressiveness, boldness, openness, activity, impulsiveness, and dominance (Travnik et al., 2020). Previous studies have utilized observational methods as well as surveys or combined different methodologies. The majority of feline behavioural studies are survey-based (Travnik et al., 2020), because cats might not behave normally in a novel test environment, making behaviour testing challenging. Personality has been studied in many different cat populations, including laboratory reared cats, homeless shelter cats, free-ranging colonies, or owned pet cats. Results of the studies investigating the structure of feline personality are summarized in Table 1. Unfortunately, several cat personality studies lack thorough validation (Gartner & Weiss, 2013).

“The Feline Five” (Litchfield et al., 2017) parallels the human Big Five personality structure (Goldberg, 1990) with the traits labelled as agreeableness, dominance, extraversion, impulsiveness and neuroticism. This framework has later been utilized in predatory behaviour (Cordonnier et al., 2023) and owner-cat relationship (Evans et al., 2019) studies. The Meet Your Match® Feline-ality™ protocol (The American Society for the Prevention of Cruelty to Animals, 2013) utilizes the dimensions of independent-gregarious and valiant scales, to match the personality types of the shelter cats and adopters. Later studies have shown the rating protocol also working in home environments (Fukimoto et al., 2020; Weiss et al., 2015). The Feline Temperament Profile (FTP) scores a cat's behaviour based on a standardized test pattern, which predicts the response to humans and cats' stress responsiveness in general (Siegford et al., 2003). Originally, the test was designed to assess the suitability of cats for nursing homes (Siegford et al., 2003). FTP has since been used when studying ocular temperature (Foster & Ijichi, 2017), cortisol concentration (Siegford et al., 2003), and paw preference (McDowell et al., 2016).

The Fe-BARQ (Feline Behavioral Assessment & Research Questionnaire) is a survey which includes items related to problematic behaviours in addition to personality (Duffy et al., 2017). The survey has been validated in English and in Spanish (Menor-Campos et al., 2021), and the online data collection is still ongoing. The survey used for the data collection of this thesis is greatly based on the Fe-BARQ (Duffy et al., 2017).

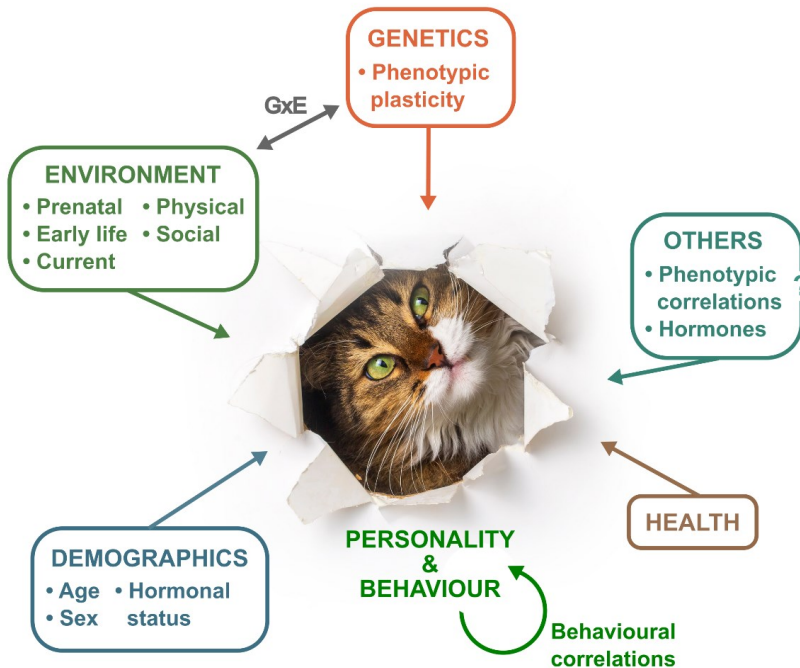
**Table 1** Summary of the 16 selected studies about personality structure in the domestic cat. N = sample size, S = survey, O = observation.

Authors	N	Traits	Sample	Methods
Ahola et al. (2017)	5726	3: Aggression, Shyness, Extraversion	Owned	S
Arahorı et al. (2016)	94	4: Openness, Friendliness, Roughness, Neuroticism	Owned	S 1,4
Bennett et al. (2017)	416	5: Playfulness, Amiability, Dominance, Demandingness, Gullibility	Owned	S 1, 2
Duffy et al. (2017)	2608	23: Playfulness/activity, Sociability, Sociability with cats, Stranger-directed aggression, Touch sensitivity/Owner-directed aggression, Fear of novelty, Trainability, and 16 others	Owned	S 1, 3
Feaver et al. (1986)	14	3: Alert, Sociable, Equable	Lab	O & S 3, 5
Finka et al. (2019)	3331	4: Gregariousness, Aggressiveness, Aloofness/avoidance, Anxiousness/fearfulness	Owned	S
Fukimoto et al. (2019)	71	3: Agreeableness, Openness, Extraversion	Shelter	S 1, 2
Gartner et al. (2014)	100	3: Dominance, Impulsiveness, Neuroticism	Shelter	S 5
Ha & Ha (2017)	251	5: Cat social, Active, Human nonsocial, Human aggressive, Intense	Owned	S
Lee et al. (2007)	196	4: Active/clever/curious/sociable, Emotional/friendly/protective, Aggressive/bad-tempered, Timid	Owned	S
Litchfield et al. (2017)	2802	5: Agreeableness, Dominance, Extraversion, Impulsiveness, Neuroticism	Owned	S 1, 2
McDowell et al. (2016)	90	2: Neuroticism, Impulsiveness	Owned	O & S
Menchetti et al. (2018)	1270	5: Sociability, Reactivity, Protectiveness, Neuroticism, Fearfulness	Owned	S 1
Stella & Croney (2019)	55	2: Shy/calm/mellow/timid, Active/playful/curious/easygoing	Owned	O & S 3
Wedl et al. (2011)	40	5: Active, Anxious, Feeding, Sociable, Rough	Owned	O 5

1 = internal consistency examined  
2 = discriminant validity examined  
3 = construct validity examined  
4 = reliability in time examined  
5 = reliability between raters examined

### 2.3.1 Factors associating with feline personality & behaviour

Similarly to other animals, cat's genetics and the environment affect the development of personality before birth (Travnik et al., 2020) (Figure 2). The individual differences in behaviour can already be seen in three-week-old kittens, as their frequency of separation calls and locomotor activity already differ at that age (Hudson et al., 2015, 2017). Studies that have investigated the effects of early life socialization to humans have found it to be very important for the cat's friendliness towards familiar and unfamiliar people, boldness, and fearfulness in the future (Casey & Bradshaw, 2008b; Lowe & Bradshaw, 2001; McCune, 1995). In addition, delayed weaning (at the age of 14 weeks or later) might be beneficial, as weaning earlier than that has been associated with aggressive behaviour and excessive grooming (Ahola et al., 2017). Other early life experiences, such as litter size and quality of maternal care, which have been shown to affect personality in dogs (Foyer et al., 2013, 2016), have not yet been studied in cats.



**Figure 2** Factors affecting personality and behaviour in cats. They are influenced by the individual's genetics, both the past and current environment and their interactions (GxE). Demographic factors, such as age and sex, contribute to personality/behaviour as well. Different health problems can change the cat's typical behaviour, e.g., the cat can become more aggressive. Personality affects behaviour, and the traits also correlate with each other. Additionally, it is likely that also other, yet uninvestigated factors in cats, such as gut microbiota and hormones, affect personality/behaviour. Finally, potential interactions exist between almost any of the mentioned factors, many health problems in cats are influenced by genetics and hormones by demographic factors or vice versa. Photo: Esin Deniz – stock.adobe.com.

The experiences later in life affect the cat's personality as well. For example, the company of other cats have been associated with decreased fearfulness and aggression toward humans (Ahola et al., 2017; Amat et al., 2009; Leech et al., 2022; Menchetti et al., 2018; Menor-Campos et al., 2021; Normando et al., 2022; Yamada et al., 2020), but enables the redirection of aggression toward other cats. Declawing (removing claws surgically) seems to decrease the cat's activity and playfulness (Duffy et al., 2017), and access to both indoor and outdoor areas seems to increase activity (Leech et al., 2022). Former stray cats have been reported to be less sociable and more aggressive toward humans than cats without this background (Ha & Ha, 2017), which may reflect the lack of beneficial contacts with humans.

The genetic background of feline personality is still mostly unknown (Travnik et al., 2020). The first genetic studies, conducted in the 1980s and 1990s, focused on the paternal effects on kittens' personality traits in free-ranging colony cats (Turner et al., 1986) and in the laboratory reared cats (McCune, 1995; Reisner et al., 1994). Turner and others (1986) found that the kittens of friendly fathers approached and touched human observers and novel objects more eagerly than the kittens of unfriendly fathers. Similarly, Reisner and others (1994) noticed that litters sired by different fathers differed in friendliness and aggressiveness (in this case response to restraining). The heritability and genetic correlations of personality traits in cats have previously been investigated in one study, which reported them to be moderate for the shyness and aggression traits (Salonen et al., 2019). In addition, the variation of the oxytocin receptor gene (OXTR) has been shown to associate with roughness (Arañori et al., 2016) and friendliness in cats (Arañori et al., 2017). Moreover, previous literature has found breed-specific differences in cats' personalities (e.g. (Ahola et al., 2017; Hart & Hart, 2013b; Naderi et al., 2011; Salonen et al., 2019; Tamimi et al., 2015; Wassink-van der Schot et al., 2016), giving indirect evidence of genetic influences on personality.

Likewise, the physiological basis of behavioural differences is largely unknown. In several animal species, the stress hormones, such as cortisol, can be used to measure the animal's physiological response to stress (Sheriff et al., 2011). In cats, however, several studies have failed to link the behavioural signs of stress with increased cortisol concentrations (Fukimoto et al., 2020; Siegford et al., 2003; J. Stella et al., 2013), thus it seems that this parameter may not be a reliable measure of stress/fear in cats. The surface body temperature may be one method to evaluate stress in cats, as cats with high ocular temperatures had lower frequencies of acceptable responses in the Feline Temperament Profile (FTP) (Foster & Ijichi, 2017), but further studies and evaluation are needed to estimate the method's validity.

Furthermore, personality is likely influenced by age, sex, and hormonal status, although studies are not unanimous. Older cats have been reported to be less active, playful, social (Gartner et al., 2014; Lee et al., 2007; Menchetti et al., 2018;

Menor-Campos et al., 2021, but see Ha & Ha, 2017), and less fearful (Ahola et al., 2017; Yamada et al., 2020) than younger cats, but having a higher probability of aggression toward strangers and other cats (Ahola et al., 2017). Sex may have an influence on aggressiveness of the cat, but studies lack consistency; some studies find males more aggressive than females (Menchetti et al., 2018; Naderi et al., 2011), but some studies have found the opposite results (Ahola et al., 2017; Arahori et al., 2017; Wassink-van der Schot et al., 2016; Yamada et al., 2020), or no difference at all (Lee et al., 2007; Tamimi et al., 2015). Furthermore, males have been reported to be less fearful in general, more social toward other cats, and less aggressive toward other cats than females (Ahola et al., 2017; Ha & Ha, 2017; Yamada et al., 2020). Intact females exhibited more aggression than sterilized females in the study of Amat and others (2009), but sterilized cats exhibited more roughness (including the adjective “aggressive”) (Arahori et al., 2017), aggression toward family members and other cats, and fearfulness toward strangers (Ahola et al., 2017) in other studies. Thus, based on these previous studies, it’s unclear whether sterilization is beneficial or harmful to the cat’s behaviour or personality.

In addition, correlations with personality and other phenotypical traits, such as coat colour, have been suggested. For example, Pontier and others (1995) suggested that orange male cats might be more aggressive than other coloured males (Pontier et al., 1995). Moreover, Stelow and others (2016) found that “orange females” (tortoiseshells and calicos), black-and-white, and grey-and-white cats exhibit more aggression than other coloured females. However, in their study, the males exhibiting the most aggression were black-and-white coloured, not orange (Stelow et al., 2016). Furthermore, in another study, orange cats were evaluated as more friendly and less shy than white and tortoiseshell cats (Delgado et al., 2012), and no differences existed in a more recent study (Leech et al., 2022). Thus, it is suggested that the relationship between the cat’s personality and the coat colour is highly influenced by the owner’s beliefs (Delgado et al., 2012), or it is a secondary effect of the breed effect (Wilhelmy et al., 2016). Additionally, it was noticed that cats without paw preference (ambilateral cats) have higher scores in neuroticism, than cats preferring the right or left paw (McDowell et al., 2016).

Personality traits also correlate with each other. For example, fearfulness correlates positively with aggression and negatively with human sociability (Ahola et al., 2017). Personality can also alter cat’s tolerance to cope with unideal environment and it is suggested that some personality types are more sensitive to stress than others (Foster & Ijichi, 2017). As prolonged stress is a common reason for problematic behaviour, cats with certain personalities, such as highly anxious cats (Normando et al., 2022), may be more prone to show problematic behaviour than others.

## 2.4 Problematic behaviour

Problematic behaviour in cats is quite common, but the exact prevalence is unknown. The majority of the Japanese cats, 78%, exhibited disturbing or very disturbing behaviour (Yamada et al., 2020), but only 15.6-20% of the European cats were reported to have one or more problematic behaviours (Finka et al., 2019; Machado et al., 2020; Normando et al., 2022). Problematic behaviour can be defined as a behaviour that is undesired for the pet owner, and it can be divided into two different categories: normal, species-typical behaviour, and abnormal, non-typical behaviour for the species (Casey & Bradshaw, 2008a). For example, scratching furniture can be problematic for the owner, but normal, healthy behaviour for the cat (J. Bradshaw, 2018). In contrast, abnormal behaviours, which usually are welfare issues for the animals, are not always considered problematic by the owners as the owner might not recognise them as problematic. The owners can, for example, feel that the abnormal behaviour, such as tail chasing in dogs is “funny” or “cute” (Burn, 2011). Moreover, even normal behaviour, which is considered problematic by owners can cause welfare issues, as it is a typical reason for relinquishment to an animal shelter and euthanasia (Salman et al., 2010; J. L. Stella & Croney, 2016). Thus, problematic behaviour can harm the emotional bond between the caretaker and the cat (Serpell, 1996), and decrease the caretaker’s satisfaction with the cat (Normando et al., 2022).

Usually, problematic behaviours occur when the cat cannot fulfil its behavioural demands (Grigg & Kogan, 2019; J. L. Stella & Croney, 2016), and problems are commonly stress-related (Amat et al., 2016). When examining all problematic behaviours together, some shared associations with environmental factors have been found. For example, problematic behaviour has been reported most often in cats acquired from pet shops (Amat et al., 2009; Grigg & Kogan, 2019) and in declawed cats (Grigg & Kogan, 2019; Martell-Moran et al., 2018). Problematic behaviours were reported less frequently in cats that had access to outdoors in two cross-sectional studies (Amat et al., 2009; Naderi et al., 2011). In addition, playing with the cat five or more minutes decreased the number of reported behavioural problems in another cross-sectional study (Strickler & Shull, 2013). Owners that had knowledge about feline behaviour reported less problematic behaviour than owners with poorer education (Grigg & Kogan, 2019), and also owners with a high score in Neuroticism reported that their cat had problematic behaviour more often than owners with a lower Neuroticism score (Finka et al., 2019). Moreover, the number of reported problems correlated with the use of aversive training methods (Grigg & Kogan, 2019), and in dogs, the use of positive punishment has been concluded to increase the risk of problematic behaviours (Ziv, 2017). Additionally, previous literature suggests that some breeds are more vulnerable to specific problems than others (J. W. S. Bradshaw et al., 1997; Overall & Dunham, 2002; Sawyer et al., 1999; Vapalahti et al., 2016), but

making conclusions based on the existing studies is hard as they have had different breed compositions.

### **2.4.1 Common problematic behaviours in cats**

Aggressive behaviour and house soiling are the most reported forms of problematic behaviours in cats (Amat & Manteca, 2019; Bamberger & Houpt, 2006). Other known forms of problematic behaviours in cats are, e.g., abnormal repetitive behaviours, such as excessive grooming. The prevalence of fearfulness as a problematic behaviour is likely underrepresented, because the owners rarely recognise fear-related behaviour in cats (Karn-Buehler & Kuhne, 2021), and owners do not consider fearfulness as irritating as other types of problematic behaviours (Normando et al., 2022).

Fearfulness is one of the traits studied in this thesis. Fear is a normal emotional response, which purpose is to get the animal to avoid potentially dangerous situations and activities (Dias et al., 2013). Thus, as a personality trait, fearfulness is a continuous trait, which can turn problematic if the fear is excessive, prolonged, or generalised in nature (Dreschel, 2010; Puurunen et al., 2020). The excessive and prolonged fear which does not necessarily have a specific object of threat is called anxiety (Dias et al., 2013). In dogs, individuals with a severe fear or anxiety disorder have been suggested to have even a shorter lifespan than dogs without that diagnosis (Dreschel, 2010). In cats, fearful behaviour includes freezing, trying to escape, and hissing, for example (Stanton et al., 2015). If a fearful cat cannot escape the fear-eliciting stimulus, fear can develop into aggressive behaviour (Rodan, 2010). The source of fear can be, e.g., unfamiliar people, conspecifics, or novel situations. Furthermore, separation anxiety is a fear-related problem, which is studied more comprehensively in dogs but exists also in cats (de Souza Machado et al., 2020; Yamada et al., 2020). Previously found associations of different factors with fearfulness have been presented in Chapter 2.3.1.

Another form of problematic behaviour studied in this thesis is aggressive behaviour, which can be described as a behaviour which purpose is to cause harm to another individual (Weinshenker & Siegel, 2002). Usually, threatening to do so is also considered as aggressive behaviour. Like fearfulness, aggressiveness is a continuous trait, and the threshold for pathological aggressiveness is ambiguous. Aggressive behaviour in cats include growling, spitting, chasing, baring teeth, and biting, for example (Stanton et al., 2015). Its motivation can be fear, frustration, maternal behaviour, predation, resource defence, or it can be petting-related (Amat & Manteca, 2019; Weinshenker & Siegel, 2002). Aggression can be directed toward different subjects, such as the owner, family members, strangers, familiar cats, unknown cats, or dogs. Aggression toward family members is an especially serious problem, and may result in euthanasia of the cat (Amat & Manteca, 2019).

In addition to the reasons mentioned previously in Chapter 2.3.1., common causes for aggressive behaviour are unknown cats, loud noises, lack of stimulation, pain, and different health problems, such as hyperthyroidism, liver dysfunction, and epilepsy (Amat et al., 2008; Amat & Manteca, 2019; Hart & Hart, 2013a).

The next investigated problem in this thesis is house soiling. House soiling, sometimes referred to as inappropriate elimination, includes both urination and defecation outside an owner-designated elimination place, although the latter is less common (Amat et al., 2009; Herron, 2010). House soiling is likely the least tolerated problem among owners (Normando et al., 2022). House soiling with urine can be further separated into marking behaviour (sometimes referred to as spraying) and latrine behaviour (sometimes referred to as inappropriate urination) (Barcelos et al., 2018). In theory, the marking behaviour serves the purpose of intra-specific communication and the latrine behaviour emptying the bladder and bowel (e.g., Herron, 2010). In practise, separating the two behaviours is challenging as the ultimate motivation for the behaviour cannot be asked from the cat. Although latrine behaviour usually happens on horizontal surfaces and marking on vertical surfaces, this rule is not a completely reliable way to differ these behaviours (Barcelos et al., 2018).

Previous literature reports numerous associations with house soiling and examined factors. Older age has been associated with house soiling in many studies (Barcelos et al., 2018 (marking only); Duffy et al., 2017; Normando et al., 2022), and some studies have found that house soiling is more common in intact cats (Hart & Hart, 2013b) and male cats (Pryor et al., 2001; Strickler & Shull, 2013). In the study of Tamimi and others (2015) having and outdoor access was associated increased house soiling, but another study disagrees with this result (Normando et al., 2022). Several health problems can cause house soiling (Carney et al., 2014; Herron, 2010; Neilson, 2004) and they should be eliminated before making an assumption of a behaviour-based problem (Herron, 2010). However, house soiling is also more common in highly anxious cats (Normando et al., 2022) and marking in less relaxed cats (Barcelos et al., 2018). In addition, litterbox related factors and litterbox management, such as the cleaning and litter type, have been associated with house soiling (Ellis et al., 2015; Herron, 2010). It has been noticed that the tolerance of poor litterbox management varies between individual cats (Herron, 2010). Some studies have reported house soiling to be more prevalent in multicat-households (Barcelos et al., 2018; Duffy et al., 2017; Pryor et al., 2001), which may be related to cleaning issues or conflicts between the cats. Moreover, house soiling is one of the typical signs of in separation-related problems in cats (de Souza Machado et al., 2020).

Lastly, abnormal repetitive behaviours (ARB) are quite rare problems, and their prevalence varies between 4.3-11.4% (Naderi et al., 2011; Tamimi et al., 2015). The most common ARBs in cats are feline hyperesthesia syndrome (FHS), psychogenic alopecia, excessive grooming or self-mutilation, wool sucking, and

pica (the consumption of unusual or non-food items)(Amat et al., 2016; Overall & Dunham, 2002; Tamimi et al., 2015). In this thesis, we focus on excessive grooming, which includes frantic licking and self-mutilation, such as pulling out hair (Overall & Dunham, 2002). In many cases, excessive grooming is not an ARB, but a sign of a health problem (S. L. Bennett & Khan, 2021), such as skin diseases, parasites, or pain (Beale, 2012; S. L. Bennett & Khan, 2021; Tilley & Smith, 2016). Other causes for excessive grooming are mostly unknown, but Ahola and others (2017) discovered that cats weaned after the age of 14 weeks exhibited less excessive grooming than cats weaned earlier than this. Moreover, in the same study, two different ARBs, wool sucking and excessive grooming, correlated with the cat's shyness and aggressiveness (Ahola et al., 2017). Similarly to other problematic behaviour, excessive grooming can be induced by environmental or social conflict, frustration, or stress (Luescher, 2003; Overall & Dunham, 2002).

### 3 Aims of the study

The overall aims of this thesis were to study the structure of feline behaviour and personality with a reliable and valid survey (study **I**) and identify potential risk factors that associate with common problematic feline behaviours: fearfulness, aggression toward humans, excessive grooming (study **II**), and house soiling (study **III**). This thesis hypothesises that the cat's personality and behaviour consist of several traits and that multiple risk factors will associate with studied problematic behaviours. The specific steps were the following:

1. Design and develop a feline behaviour and personality online survey for data collection from Finnish cat owners. In addition to behavioural section, the survey will include comprehensive background and health sections.
2. Study behaviour and personality structure by utilizing explorative factor analyses.
3. Validate the survey and founded traits with comprehensive set of reliability and validity measures.
4. Identify potential risk factors for common problematic behaviours from over 30 variables using generalized linear models with model selection. Identify potential risk factors for common problematic behaviours from over 30 factors concerning demographical, environmental, and health variables as well as personality and behaviour traits. This will be done by utilizing generalized linear models with model selection. The importances of the founded associating risk factors will be estimated by calculating relative and absolute importance.

## 4 Materials and methods

### 4.1 Ethical statement

The study was conducted according to the guidelines of the Declaration of Helsinki and approved by the University of Helsinki Viikki Campus Research Ethics Committee (February 11, 2019). Informed consent was obtained from all respondents.

### 4.2 The survey and data collection

We developed a feline behaviour and personality survey based on the previous behavioural surveys. One of the most important sources was the Fe-BARQ (Feline Behavioural Assessment and Research Questionnaire)(Duffy et al., 2017). Those survey items in the Fe-BARQ had been selected based on a comprehensive literature review concerning full spectrum of cat behaviour and behavioural problems and the list was then commented by five experts on cat behaviour (Duffy et al., 2017). We modified the items to be more suitable for Finnish cat population, as, for example, in Finland declawing and selling cats in pet shops are illegal. We also translated the statements to Finnish to avoid possible misunderstandings, as the majority of the Finnish people are not fluent in English. To improve the survey further, we invited nine cat behaviour, welfare, and health experts such as veterinarians and breeders, to review and comment on the survey. The final version of the survey included three sections: behaviour, background, and health (Supplementary Material, study I (Mikkola, Salonen, Hakanen, et al., 2021)).

The behaviour section consisted of 138 statements in a randomized order. Answering options for these statements were “strongly disagree”, “somewhat disagree”, “neither agree nor disagree”, “somewhat agree”, “strongly agree” and “I do not know”. The background section included questions about the time before the cat’s weaning and about the current physical and social environment. The health section listed common health issues in cats, and the owner was asked to choose the ones their cat had. Choosing a health issue opened up additional questions about the severeness and frequency of the problem. The survey was published on the Petsofi platform (*Petsofi Ltd*) and signing up on the platform was obligatory to participate in the study. The mandatory information for registering included the owner’s email address, first name, last name, and country.

Furthermore, they could fill in, e.g., the official name and nickname of their cat, cat's gender, breed, date of birth, registry ID, and registry (FIFE, CFA, TICA or WCF).

Our target group were adults who currently owned one or multiple cats. We advertised the survey in a pet fair, on our social media pages, and in cat magazines (Figure 3) with the help of cat and breed organizations, such as Suomen Kissaliitto ry (a Finnish cat association). In addition, we developed an automatic behaviour and personality report for study participants to boost study participation.



**MITEN HYVIN TUNNET KISSAYSTÄVÄSI?**

Osallistu käyttäytymistutkimukseen ja opi lisää kissasi persoonallisuudesta.

Tutkimuksen tavoitteena on oppia ymmärtämään kissojen käyttäytymistä ja parantaa niiden hyvinvointia.

Käyttäytymiskyselyn vastausten perusteella kissallesi luodaan persoonallisuusprofiili ja voit verrata kissasi profiilia rodun ja kaikkien kissojen keskimääriäisiin tuloksiin.

Osallistumisohjeet:

- 1) Rekisteröidy Petsofiin osoitteessa [petsofi.fi](https://petsofi.fi)
- 2) Lisää kissasi painikkeella "Lisää eläin" ja täytä sen tiedot
- 3) Klikkaa kissasi kuvaa ja klikkaa Analyysit-osiossa kohtaa "Kissojen persoonallisuuskysely"

Tutkimus on toteutettu Kissojen geenitutkimusryhmässä Helsingin yliopiston ja Folkhälsanin tutkimuskeskuksen alaisuudessa.



**Figure 3** An example of an advertisement published in Finnish cat magazines. Photo: Daria Minaeva – shutterstock.com. Design: Milla Salonen.

The data collection started in March 2019 and ended in September 2020. In addition to this dataset, we collected two other datasets to evaluate test-retest

(Jan–Nov 2020) and inter-rater (Aug–Jan 2021) reliabilities. For those, we contacted the owners who participated in the study 1–3 months ago via email and asked them to answer the behaviour section again or ask an adult person living in the same household to answer this section about the same cat. From the second raters, we also asked how long they had known the cat. The answering options were “less than 3 months”, “3–6 months”, “6 months to 1 year”, “1–5 years”, and “over 5 years”.

### 4.3 Subjects

We collected data of 4492 cats. After excluding duplicates or entries with insufficient data, e.g., high individual-level missingness in the behaviour section (>20%), we ended up with the final sample size of 4316 cats for the study **I**. In addition to cats being alive during the participation, we also included cats that had deceased less than three months before the time of participation. For the studies **II** and **III**, we also needed the background and health information of the cat. Due to missing data, some entries had to be excluded. Therefore, the datasets in the studies **II** and **III** included fewer cats, 3255 and 3048, respectively.

The study population included cats from 56 different breeds as well as house cats and mixed-breed cats. To achieve meaningful group sizes, we had to combine the data of some breeds. The combining of breeds was based mostly on the breeds’ shared genetic history (Gandolfi et al., 2018; Lipinski et al., 2008; Menotti-Raymond et al., 2008). The landrace cats in this study are cats derived from locally adapted Finnish cat populations and (should) not have breed ancestry. The landrace cats were divided into short- and longhaired landrace cats, as their sample size enabled that distinction, even though they can be born in the same litter. The “house cat” group included house cats (non-purebred cats with a purebred ancestor or apparent breed-specific characteristics) and mixed-breed cats. Finally, the “other breeds” group included breeds that were not easily combined with any other breeds and had only few individuals ( $N < 34$ ). The same categorization was used in all studies.

Almost half of the cats were females (49%) (studies **I-III**). The majority of the cats were sterilized or neutered (~70%, study **I**), or sterilized, neutered, or were being administered medical contraception (~90%, studies **II** and **III**). The mean age was 6 years, the youngest cat was three months old and the oldest was 22 years old (studies **I-III**).

### 4.4 Construction of explanatory variables

The basic information of the cat, i.e., *breed* and *sex*, were taken from the cat’s profile information during study **I**. We calculated the age based on the cat’s date of birth and the date the behaviour section was answered. In the cases where the cat

had already deceased, the age was calculated based on the date of death. These variables were utilized in studies **II** and **III** as well.

We formed 17 new variables for study **II**. These variables were named hormonal status, number of siblings, socialization to humans, socialization to animals, place where the cat was acquired from (acquisition place hereafter), main reason for getting the cat, food type, feeding style, number of large scratching trees, number of small scratching trees, playtime frequency, type of outdoor access, average number of days the cat is left alone during the week, hobbies, number of other cats in household (other cats in household hereafter), owner's previous cat experience/ownership, and time since last vet visit. For study **III**, we utilized some of these existing variables and formed nine new ones, i.e., age at sterilization, number of litter boxes, living space, dogs in a family, children in a family, urinary tract disease, diseases causing excessive drinking, intestinal disease, and musculoskeletal disease. We had to transform some initially numeric variables, such as the number of small scratching trees, to categorical variables as they had remarkably high missingness. For the same reason, we also had to combine some groups and questions to new variables.

*Socialization to humans* variable was a combination of two questions: “how often the cat met unfamiliar adults at the age of 0–12 weeks” and “how often the cat met unfamiliar children at the age of 0–12 weeks”. It had four possible categories “poor” (the cat met both unfamiliar adults and children on a couple of occasions or not at all); “moderate” (the cat met unfamiliar adults weekly or daily, but children on only a couple of occasions or not at all, or vice versa, or one question was left blank while the response to the other question was weekly or daily); “good” (the cat met both unfamiliar adults and children weekly or daily); and “unknown” (both questions were unanswered or the response to one question was not at all while the other question was left blank).

*Type of outdoor access* variable was transformed from a multiple-choice question. The options to choose from were “freely unsupervised”, “freely supervised”, “on a leash”, “in a fenced backyard or outdoor cage”, “on a balcony”, and “my cat does not have access to the outdoors”. This was simplified to categories: “none” (cat did not have access to the outdoors), “balcony” (cat only had access to a balcony), “on a leash” (cat had access to the outdoors only while on a leash or had access both on a leash and to a balcony), “in a cage or freely supervised” (cat had access to the outdoors in a fenced backyard, outdoor cage, or freely but supervised, with or without access to a balcony or on a leash), and “freely unsupervised” (cat had access to the outdoors freely unsupervised, with or without any other access type).

*Acquisition place* variable had the categories “rescue”, “breeder”, “previous owner”, and “born in the household”. The “rescue” group included cats adopted from an Animal Welfare Association/shelter as rescues, as well as cats obtained directly from barns, streets etc. *Main reason for getting the cat* variable had the

categories “family member”, “pet”, and “breeding/show/work”. Only few cats were taken primarily to work (= hunt rodents). *Other cats in the household* was initially a numeric variable, but it was transformed to the categories “none”, “one other”, “two other”, and “three or more other”. Another initially numeric variable, *children in the family*, was transformed into a binary variable and therefore had the categories “yes” and “no”.

*Time since last vet visit* variable described the time since last veterinarian visit and had the categories “less than 6 months ago”, “6–12 months ago”, “1–2 years ago,”, and “over 2 years ago”. Also, cats that had never visited a veterinarian (N = 14) or whose owners had not filled the health section, were placed in the “over 2 years ago” category.

*Hormonal status* variable had two categories “intact” and “sterile” (includes both physically and chemically sterilized cats). In study **III**, we used *age at sterilization* variable instead of *hormonal status*, as previous literature has hypothesized that age of sterilization can affect house soiling (Spain et al., 2004). *Age at sterilization* included the categories “intact”, “less than 4 months old”, “4 months–1 year old”, “over 1 year old”, and “unknown”.

Health information of the cat was simplified to a *health problems* variable for study **II** that had three categories: “yes” (at least one of the selected problems was severe and potentially influenced the daily life and behaviour), “no”, and “unknown” (the health section was not filled). The diseases and severeness that led to the categorization of a cat into “yes” or “no” categories are explained in the Supplementary Table of the study **II** (Mikkola et al., 2022). For study **III**, we wanted more specific health variables as some health problems, such as urinary tract infections and diabetes, may cause house soiling (Horwitz, 1997). Thus, we formed the variables *urinary tract disease*, *diseases causing excessive drinking*, *intestinal disease*, and *musculoskeletal disease*. All health variables included the categories “yes”, “no”, and “unknown” (cats missing the health information). More detailed explanations of the explanatory variables can be found in previous publications (Mikkola et al., 2022, 2023; Mikkola, Salonen, Hakanen, et al., 2021).

## 4.5 Statistical analyses

### 4.5.1 Personality and behaviour structure, validity, reliability, and breed differences (study I)

We performed an explorative factor analysis (EFA) to reduce the large number of behaviour statements into biologically meaningful traits using polychoric correlation matrices. We tested that the dataset was appropriate for EFA with the Kaiser-Meyer-Olkin test for sampling adequacy and with Bartlett’s test of sphericity from the package *psych* (Revelle, 2021). We estimated the optimal

number of factors with the scree test, parallel analysis, Velicer's minimum average partial (MAP) test, and by extracting structures with 1 to 11 factors (Goldberg's hierarchical tree). Because some cats had missing data, we used mean imputation. Rotation was not used. The dataset used here included 4316 cats.

We calculated correlations between the first and second times of answering to evaluate test-retest reliability, and the intraclass correlation coefficients (ICC) to evaluate inter-rater reliabilities. ICC can be measured in different ways and the suitable versions for our study design were ICC(1,1) (each subject is rated by different a rater, reliability calculated from a single measurement) and ICC(1,k) (each subject is rated by different a rater, reliability calculated from the mean ratings of  $k$  raters) (Revelle, 2021; Shrout & Fleiss, 1979). Next, we removed unreliable items (statements) based on their reliabilities. There are no established guides for the cut-offs of test-retest and inter-rater reliabilities, and thus, we decided to remove only the items with ICCs close to zero ( $ICC(1,1) < 0.08$ ,  $ICC(1,k) < 0.13$ ). The test-retest correlations were acceptable for the rest of the items, so no item were removed due to poor correlation. The removed items can be found in the Supplementary material of Mikkola and others (2021).

Then, we removed non-loading items ( $< |0.3|$ ) one by one, constantly re-running the factor analysis after removing an item, as suggested in the study of Maskey and others (2018). After this, we estimated the internal consistency, test-retest reliability, and inter-rater reliability for the final factor structure. We estimated the factors' internal consistency with Cronbach's alpha and Guttman's lambda.

We used the correlation-preserving factor score estimation method (method = "tenBerge") to calculate scores for individual cats and utilized these scores in convergent validity testing and later analyses. In convergent validity testing, we formed hypotheses based on the previous literature. We hypothesized, for example, that male cats had more litterbox issues, but were less fearful than female cats (Ahola et al., 2017; Hart & Hart, 2013b; Strickler & Shull, 2013). All hypotheses are shown in study I (Mikkola, Salonen, Hakanen, et al., 2021).

Lastly, we studied whether the breed groups differed in factor scores using Kruskal-Wallis tests in the study I. The significance cut-off P-value was set at  $P < 0.05$ , and all P-values were corrected for false discovery rate (FDR) with Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995). All statistical analyses above were conducted in R (R Core Team, 2021), utilizing the package *psych* (Revelle, 2021).

#### **4.5.2 Model selection of fearfulness, aggression toward humans, and excessive grooming (study II)**

We used generalized linear models (GLM) to examine associations of personality and behaviour traits, demographic variables, and environmental variables with

fearfulness, aggression toward humans, and excessive grooming. We selected this approach as the studied traits were non-normally distributed, and therefore, linear regression was not appropriate. Using GLMs with multiple explanatory variables in the same model enables the observation of their independent influence on the studied traits. The most suitable distribution, which was the gamma distribution with the log-link function, was selected based on visual inspection of residual using the packages *rcompanion* (Mangiafico, 2019) and *boot* (Canty & Ripley, 2021). The dataset used in this study (II) included 3255 cats, and the personality and behaviour scores were based on the factor scores from study I.

We had a high number of explanatory variables. Therefore, we used 5-fold cross-validation to find the most important variables for each problematic behaviour. We divided the initial dataset into five smaller subsets, which each included ~80% of the cats (  $N = 2603-2605$ ) using the package *caret* (Kuhn, 2021). The best models for each dataset were selected using the forward stepwise Akaike Information Criterion (AIC) approach utilizing the package *airGLMs* (Niskanen et al., 2021). The base model included sex, age, and breed. Additionally, the potential two-way interactions between variables were included in the model selection. Altogether, we obtained five models for each trait, i.e., fearfulness, aggression toward humans, and excessive grooming. From these models, we selected only the variables occurring in every model of the specific trait. The number of explanatory variables was still high; thus, we inspected their relative influences in the models with generalized boosted regression models from the package *gbm* (B. Greenwell et al., 2020). Instead of P-values, generalized boosted regression models report relative influences for the explanatory variables in the models. We noticed that some variables, e.g., hormonal status and hobby in the fearfulness model, had very low relative influences, and we decided to exclude them from the final models.

### **4.5.3 Model selection of house soiling and litter box fussiness models (study III)**

We decided to conduct a new EFA for statements related to the house soiling/litterbox issues, instead of using the existing litterbox issues factor, because we wanted to study the problem in more detail. The statements included to this new analysis were: cat urinates in inappropriate places, sprays indoors, defecates in inappropriate places indoors, refuses to use the litter box if it is dirty, does not want to use the same litter box as other cats in the household, and prefers specific types of cat litter. Before the EFA, we excluded individuals with over 20% missingness in total in the remaining statements, which led to a dataset of 3048 cats.

We conducted the EFA in a similar way as in the study **I**. Therefore, we started with testing the appropriateness of our dataset for explanatory factor analysis, by a polychoric correlation matrix, without the use of rotation, and we used mean imputation for missing data. Similarly, the optimal number of factors was selected utilizing the scree test, parallel analysis, Velicer’s minimum average partial (MAP) test, and by extracting structures with 1 to 3 factors (Goldberg’s hierarchical tree). The structure with two factors was the best. The first factor, house soiling, consisted of three items: cat urinates in inappropriate places, sprays indoors, and defecates in inappropriate places indoors. The second factor, litterbox fussiness, also included three items: cat refuses to use the litter box if it is dirty, does not want to use the same litter box as the other cats in the household, and prefers specific types of cat litter. The “TenBerge” estimation method was also used here to extract factor scores for individual cats.

We had a high number of potential explanatory variables ( $N = 34$ ), thus, to exclude the least important ones, we calculated their relative influences both for all selected statements independently and for the two factors, using the package *gbm* (B. Greenwell et al., 2020). We excluded variables with a relative influence of less than one in any of the models before the next model selection phase.

Similarly to study **II**, we utilized generalized linear models to identify the explanatory variables that had associations with studied traits. Again, both factors were non-normally distributed, and we found a more suitable distribution for them (the gamma distribution with the log-link function) with the packages *rcompanion* (Mangiafico, 2019) and *boot* (Canty & Ripley, 2021).

Next, we performed the repeated train-test validation by randomly splitting the data five times into training (50% of data) and testing (50% of data) datasets with the package *caret* (Kuhn, 2021), resulting in ten smaller datasets ( $N = 1524-1525$ ). Then, we performed a forward stepwise AIC model selection utilizing the package *airGLMs* (Niskanen et al., 2021) for each dataset and both factors. Here, the base model included only sex and age. We calculated the number of times each variable was included in the models and formed the final models for both traits by only including variables that were included in at least 90% of the models.

#### **4.5.4 Model fit and extraction of the results (studies II & III)**

We assessed the model fit of each final model carefully, starting with the examination of the linearity of continuous variables with generalized additive models using the package *gam* (Hastie, 2020). In the fearfulness model, the explanatory variables age, litterbox issues, excessive grooming, and aggression toward humans did not meet the linearity assumption. In the aggression toward humans model, the variables age, excessive grooming, litter box issues, and sociability toward cats did not meet the assumption. In the excessive grooming model, the age, aggression toward humans, and litter box issues did not meet the

assumption. In house soiling model, age and sociability toward cats did not meet the assumption. Finally, in litter box fussiness model, age, fearfulness, and activity/playfulness did not meet this assumption. For the variables that did not meet this assumption, we added both linear and quadratic variables to the models and inspected the models' linearity again. This decreased the linearity of some variables further, thus, we did not add them as quadratic in the final models. For example, in the fearfulness model we added the litterbox issues and aggression toward humans as both linear and quadratic variables (litterbox issues<sup>2</sup> and aggression toward humans<sup>2</sup>) but did not do this to the excessive grooming for the reason given previously.

Next, we visually examined the residuals of the final models and inspected the presence of heteroscedasticity with the packages *rcompanion* (Mangiafico, 2019) and *boot* (Canty & Ripley, 2021). We searched possible outliers with the packages *broom* (Robinson et al., 2021), *dplyr* (Wickham et al., 2021), and *ggplot2* (Wickham, 2016). Several outliers were found, and we compared the model with and without them. The results of any models did not markedly differ, and the observations were real, so we kept them in the data. Then, we evaluated multicollinearity of the explanatory variables with the variance inflation factor (VIF) using the package *car* (Fox & Weisberg, 2019) and assessed the general fit with the Durbin-Watson test using the package *lmtest* (Zeileis & Hothorn, 2002).

Finally, we performed an analysis of variance (ANOVA) to obtain the overall effect of the explanatory variables with the package *car* (Fox & Weisberg, 2019). We also calculated the estimated marginal means for categorical and binary variables using the package *emmeans* (Lenth, 2021), and obtained the means and confidence limits of the continuous variables using the package *effects* (Fox, 2003; Fox & Weisberg, 2019). P-values were corrected for false discovery rate and the significance cut-off P-value was set at  $P < 0.05$ .

#### **4.5.5 Importance of the variables (studies II & III)**

We wanted to evaluate the importance of the variables included in the models and thus, we inspected the relative effect size with variance-based variable importance utilizing a feature importance ranking measure approach from the package *vip* (B. M. Greenwell & Boehmke, 2020). The variable importance was scaled, and the most important variable in each model therefore reached a score of 100. In addition, we calculated the partial Cohen's  $f^2$  to inspect absolute effect sizes using the package *effectsize* (Ben-Shachar et al., 2020). Effect sizes for the study **II** were calculated after the publication, thus the results are not part of the publication itself and are shown only part of this thesis. All analyses for studies **I** and **II** were made in R 4.1.1 and for the study **III** in R 4.1.2 (R Core Team, 2021).

## 5 Results

### 5.1 Behaviour and personality structure, reliability, and validity

The factor structure with seven factors was the most consistent and it accounted for 43% of the variance in behaviour and personality. Based on the items loading into the factors, we named the factors activity/playfulness, aggression toward humans, sociability toward humans, sociability toward cats, excessive grooming, and litterbox issues (Table 2).

**Table 2** Feline personality and behaviour traits with the loading items. Item names are abbreviated from the original statements. Items listed first had the highest absolute loadings and the last had the lowest loadings (from up to down and left to right). Items with loadings  $\geq|0.3|$  were considered as loading. + = positive loading, - = negative loading. N = 4316.

---

<b>Fearfulness</b>	
+ Escapes or hides from unfamiliar people	+ Is easily scared even by small, unexpected things and sounds
- Is comfortable and relaxed among people in social gatherings	+ Freezes when examined or treated by a veterinarian
- Always greets unfamiliar adults visiting your home in a friendly manner	+ Shows restlessness or fearfulness when unfamiliar objects are introduced into the home
+ Does not approach people visiting his/her home right away	- Seems confident at home
- Is comfortable and relaxed when being petted by unfamiliar people	+ Runs or hides when hearing a sudden or loud noise coming from outside the house
- Appears comfortable when playing with unfamiliar people	+ Shows restlessness or fearfulness when home is modified
- Always greets unfamiliar children visiting your home in a friendly manner	+ Hides or escapes when a household member prepares to leave
- Seems comfortable and confident in unfamiliar places outside the home	+ Growls or hisses at unfamiliar adults
+ Runs or hides when hearing a sudden or loud noise coming from inside the house	+ Growls or hisses when an unfamiliar person tries to touch or pet him/her
	+ Stares intensely at unfamiliar people

---

---

**Activity/playfulness**

---

- |   |  |
|---|--|
| <ul style="list-style-type: none"><li>+ Stalks, chases or pounces on moving objects</li><li>+ Runs around in the house while playing</li><li>+ Active, does not spend long time idle</li><li>+ Carries small objects or toys in his/her mouth</li><li>+ Initiates interactive play with people</li><li>+ Enjoys jumping and climbing to high places</li><li>+ Gets excited about new toys</li><li>+ Plays fetch with people</li><li>+ Gets excited when looking at birds or other small animals at the window</li><li>+ Often exhibits sudden bursts of running ("zoomies")</li><li>+ Quickly finds new ways to get attention</li><li>+ Chases or follows shadows or lights</li><li>+ While playing, always chases and ambushes other household members playfully</li></ul> | <ul style="list-style-type: none"><li>+ Chases rodents, birds, insects or other small animals</li><li>+ Reacts to the video or sound coming from the TV or computer screen</li><li>+ Rests or sleeps in elevated places</li><li>+ Quickly learns to associate separate things</li><li>+ Walks to the hallway/next to front door when a household member prepares to leave</li><li>+ Moves elegantly and gracefully</li><li>+ Always comes to the hallway/next to front door when a household member arrives home</li><li>+ Chases or hunts imaginary objects</li><li>+ Is persevering, persistent and determined. Does what he/she wants even if he/she is told not to</li></ul> |
|---|--|

---

**Aggression toward humans**

---

- |  |   |
|--|---|
| <ul style="list-style-type: none"><li>+ Attempts to scratch or bite when his/her nails are clipped</li><li>+ Attempts to scratch or bite when given medicine by a familiar person (this do not include vets)</li><li>+ Growls or hisses when given medicine by a familiar person (this does not include vets)</li><li>+ Growls or hisses when his/her nails are clipped</li><li>+ Attempts to scratch or bite when examined or treated by a veterinarian</li><li>+ Growls or hisses when petted at the base of the tail</li><li>+ Attempts to scratch or bite when being brushed</li><li>+ Attempts to scratch or bite when petted at the base of the tail</li><li>+ Attempts to scratch or bite (in a non-playful way) when petted on the belly</li></ul> | <ul style="list-style-type: none"><li>+ Unexpectedly scratches or bites when petted</li><li>+ Growls or hisses when examined or treated by a veterinarian</li><li>+ Growls or hisses when an unfamiliar person tries to touch or pet him/her</li><li>+ Growls or hisses when approached by human while in possession of prey</li><li>+ Chases or bites people's moving legs or feet (in a non-playful way)</li><li>+ Growls or hisses at unfamiliar adults</li><li>+ Attempts to scratch or bite a familiar cat when the familiar cat is staring, growling, or hissing at him/her</li><li>+ Squirms and tries to escape when picked up and held in arms</li></ul> |
|--|---|

---

**Sociability toward humans**

---

- |   |   |
|---|---|
| <ul style="list-style-type: none"><li>+ Often seeks out physical contact from people</li><li>+ Always purrs when petted</li><li>+ Purrs when sitting on someone's lap (has jumped up voluntarily)</li><li>+ "Talks" to people</li><li>+ Human-oriented: Enjoys the company of people more than the company of other cats</li><li>+ Reacts to different events and stimuli by vocalizing</li><li>+ Shows restlessness when a household member prepares to leave the home</li></ul> | <ul style="list-style-type: none"><li>+ Comes when called</li><li>+ Shows restlessness when a member of the household shows affection to another pet</li><li>+ Vocalizes when left alone at home</li><li>+ Tends to lie on newspapers or other things that are being used by people</li><li>+ Shows restlessness when a member of the household shows affection to a person</li><li>– Squirms and tries to escape when picked up to the lap of a sitting person</li></ul> |
|---|---|
-

<b>Sociability toward cats</b>	
+ Seeks company of other cats in the household	– Growls or hisses at a familiar cat when the familiar cat is staring, growling, or hissing at her/him
+ Seeks physical contact from other cats	
+ Enjoys playing with other cats	– Attempts to scratch or bite a familiar cat when the familiar cat is staring, growling, or hissing at him/her
+ Gets along well with other cats in the household	
– Growls or hisses when approached by a familiar cat in a favourite resting place	
– Human-oriented	
<b>Excessive grooming</b>	
+ Shows excessive and intensive grooming throughout the day	+ Exhibits sudden frantic licking or chewing his/her body
+ Exhibits self-mutilation	
<b>Litterbox issues</b>	
+ Urinates (crouching position) in inappropriate places	+ Sprays (standing position with tail raised vertically and vibrating) indoors
+ Defecates in inappropriate places indoors	+ Prefers specific types of cat litter
+ Refuses to use the litter box if it is dirty	
+ Does not want to use the same litter box than the other cats in the household	

We evaluated the internal consistency with both Cronbach's alpha and Guttman's lambda 6. Cronbach's alpha varied from 0.60 (litterbox issues) to 0.90 (fearfulness) and Guttman's lambda 6 from 0.60 (excessive grooming) to 0.93 (fearfulness) (Table 3). Test-retest reliabilities varied from 0.69 (excessive grooming) to 0.92 (aggression toward humans) and inter-rater reliabilities from 0.75 ICC<sub>1,k</sub> (aggression toward humans) to 0.93 ICC<sub>1,k</sub> (excessive grooming).

**Table 3** Internal consistency, test-retest reliability, and inter-rater reliability of feline behaviour and personality factors. ICC = intraclass correlation coefficient. N = 4316.

<b>Factor</b>	<b>Internal consistency</b>		<b>Test-retest reliability</b>	<b>Inter-rater reliability</b>	
	Cronbach's alpha	Guttman's lambda 6	Correlation	ICC <sub>1,1</sub>	ICC <sub>1,k</sub>
Fearfulness	0.90	0.93	0.91	0.65	0.79
Activity/playfulness	0.84	0.87	0.89	0.65	0.78
Aggression toward humans	0.83	0.88	0.92	0.61	0.75
Sociability toward humans	0.70	0.76	0.82	0.71	0.83
Sociability toward cats	0.83	0.86	0.78	0.72	0.84
Excessive grooming	0.66	0.60	0.69	0.87	0.93
Litterbox issues	0.60	0.61	0.81	0.83	0.91
Mean	0.77	0.79	0.83	0.72	0.83

We formed 25 hypotheses to test the survey's convergent validity and met 22 of them. The rejected hypotheses were 1) male cats have more litterbox issues than females, 2) cats living in multicat households have more litterbox issues than single cats, and 3) cats with owner-reported problematic behaviour are less social toward humans than other cats. To assess the discriminant validity, we studied the factor correlations and found only one moderate correlation, which occurred between sociability toward cats and aggression toward humans ( $-0.31$ ). Based on these estimates, we can say that the survey was both valid and reliable. Therefore, we decided that the further use of the survey and the collected data is justifiable and meaningful.

## 5.2 Factors associated with problematic behaviours

We found several associations between studied problematic behaviours and risk factors. Some of them were problem-specific, but the majority were associated with more than one problem (Figure 4).

Variable	Trait				
	Fearfulness	Aggression tow. humans	Excessive grooming	House soiling	Litterbox fussiness
Age	∩				+
Sex	•	•		•	
Breed	•	•	•	•	
Hormonal status					
Age at sterilization				•	
Fearfulness		+	+	+	+
Activity/playfulness		+			∩
Aggression toward humans	+		+		
Sociability toward humans	-	-	+		
Sociability toward cats		-		-	
Excessive grooming	+	∩			
Litterbox issues	∩	∩	∩		
Main reason for getting cat	•				
Acquisition place	•	•			
Siblings					
Socialization to animals					
Socialization to humans	•				
Other cats in household	•	•			
Children in the family					•
Dogs in the family					
Playtime frequency					
Type of outdoor access	•		•		
Number of litterboxes					
Living space					
Hobby					
Large scratching trees					
Small scratching trees					
Feeding style					
Food types					
Days cat is left alone during week					
Owner's previous cat experience					
Time since last vet visit		•			
Health problems			•		
Urinary track disease				•	
Diseases causing excessive drinking					
Intestinal disease					
Musculoskeletal disease					

**Figure 4** Studied explanatory variables in the model validation processes of the feline problematic behaviours. Dark grey = in the final model, light grey = tested but not included in the final model, white = not included in the model validation. Symbols = statistically significant positive (+), negative (-), or nonlinear (∩, U, •) association (P < 0.05).

### **5.2.1 Personality and behaviour correlates**

Personality and behaviour traits correlated greatly with each other. Especially, fearfulness correlated with all other problematic behaviours. The correlations were positive; when the fearfulness score of the cat increased so did aggression toward humans, excessive grooming, house soiling, and litterbox fussiness scores.

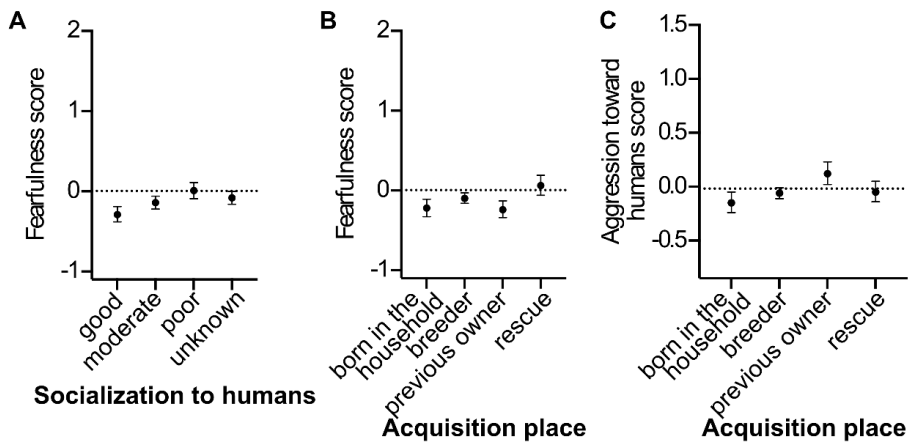
Activity/playfulness correlated positively with aggression toward humans, and litterbox fussiness. As an explanatory variable, aggression toward humans correlated positively with fearfulness and excessive grooming. Sociability toward humans correlated negatively with fearfulness and aggression, but positively with excessive grooming. Sociability toward cats correlated negatively with aggression and house soiling. Excessive grooming correlated positively with fearfulness and had a nonlinear association with aggression.

Litterbox issues correlated positively with fearfulness and had nonlinear associations with aggression and excessive grooming. House soiling score correlated positively with fearfulness and negatively with sociability toward cats. Finally, the litterbox fussiness score correlated positively with fearfulness and activity/playfulness.

## 5.2.2 Environmental factors of behaviour

### 5.2.2.1 Early life conditions

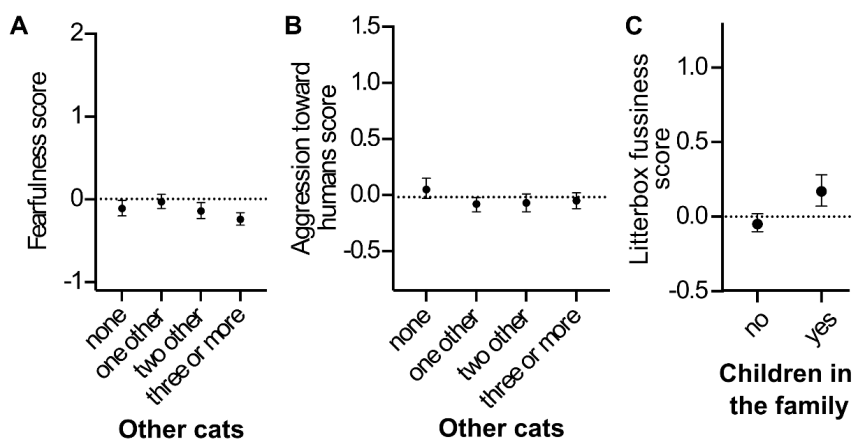
Several environmental factors associated with studied problematic behaviours. Some of the early life factors, i.e., socialization to humans, animals, siblings, and acquisition place associated with fearfulness and aggression toward humans. Cats with poor or moderate early life socialization to humans during the socialization period (at 0–12 weeks of age) were, on average, more fearful than cats with good socialization (Figure 5A). In addition, rescue cats were more fearful than cats obtained from a previous owner, from a breeder, or cats still living in their birth home (Figure 5B). Interestingly, cats obtained from a previous owner were less fearful than cats taken from a breeder (Figure 5C). However, cats acquired from a previous owner were more aggressive toward humans than cats acquired elsewhere. We found no associations of socialization to animals or siblings variables with problematic behaviours.



**Figure 5** Association of A) socialization to humans, and B) acquisition place with fearfulness, and C) acquisition place with aggression toward humans. Error bars indicate 95% confidence limits. N = 3255.

### 5.2.2.2 Current environment & environmental enrichment

Factors focusing on the current social environment, i.e., number of other cats in the household, dogs or children in a family, associated with some of the problematic behaviours as well. Cats living with three or more cats were less fearful than cats living with one cat or as the only cat (Figure 6A). In addition, cats living with one or two other cats were less aggressive than cats living as the only cat (Figure 6B). We examined the possible associations of children and dogs in the family only in the study **III**, and found that the existence of children, but not dogs, associated with increased litterbox fussiness (Figure 6C).



**Figure 6** Association of A) fearfulness, and B) aggression toward humans with the number of other cats in the household, and C) litterbox fussiness with children in the family. Error bars indicate 95% confidence limits. N = 3255 (A & B) and 3049 (C).

In addition, the type of outdoor access associated with fearfulness and excessive grooming. Cats going outdoors on a leash or freely unsupervised were less fearful than cats with access only to a balcony, outdoor freely supervised, in a cage, or not having an access at all. Moreover, cats with an access to an outdoor cage, going outdoor freely unsupervised, or supervised exhibited less excessive grooming than cats with access only to a balcony, outdoor on a leash or without any access type.

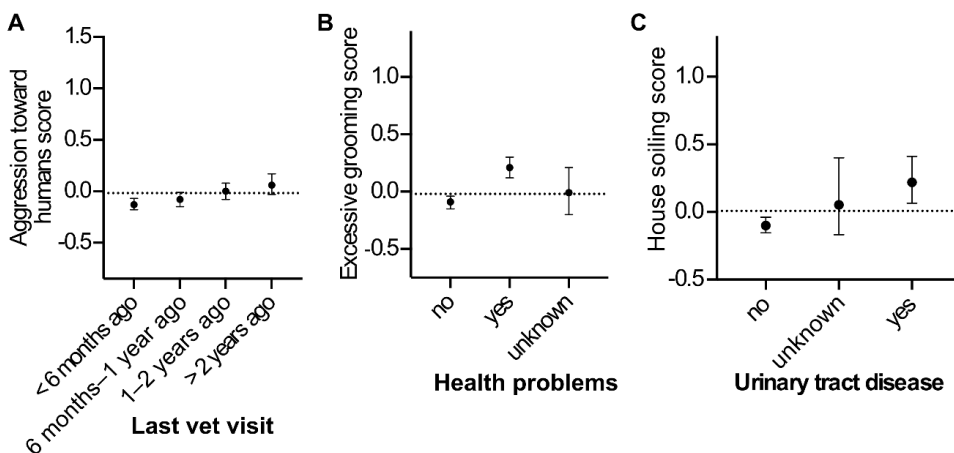
Associations of the number of litterboxes were examined in study **III**, but not in study **II**. Number of litterboxes was included in the final model of house soiling, but after the correction of P-values for FDR, only one statistically significant contrast remained: cats in the households with only one litterbox exhibited less house soiling than cats in the households with four or more litterboxes.

Finally, the results suggested that playtime frequency may associate with house soiling; we noticed a trend that playing with a cat less than weekly was associated with a higher chance of house soiling compared to playing with a cat several times during a day ( $P = 0.055$ ). Living space and the factors hobby, large scratching trees, small scratching trees, feeding style, food types, and days the cat is left alone during the week did not associate with any of the problematic behaviours.

### 5.2.2.3 Owner & health-related factors

Owner's primary reason for getting the cat was associated with fearfulness as cats obtained for breeding, cat shows, or to work were less fearful than cats acquired as pets or family members. Owner's previous cat experience or ownership did not associate with any of the problematic behaviours.

Time since the last vet visit was associated with aggression toward humans: Cats that were taken to a veterinarian more than two years ago or never scored higher than cats taken to a veterinarian under one year ago (Figure 7A). In addition, cats taken to a veterinarian one to two years ago scored higher in aggression than cats taken to a veterinarian less than six months ago. Moreover, cats that had health problems exhibited more excessive grooming than cats without them (Figure 7B), but the health status did not associate with fearfulness or aggression toward humans. In study III, we used urinary tract disease, diseases causing excessive drinking, intestinal disease, and musculoskeletal disease variables, instead of the health problems variable. From those, we found only one significant association: Cats with urinary tract disease history scored higher in house soiling than cats without them ( $P < 0.001$ )(Figure 7C).



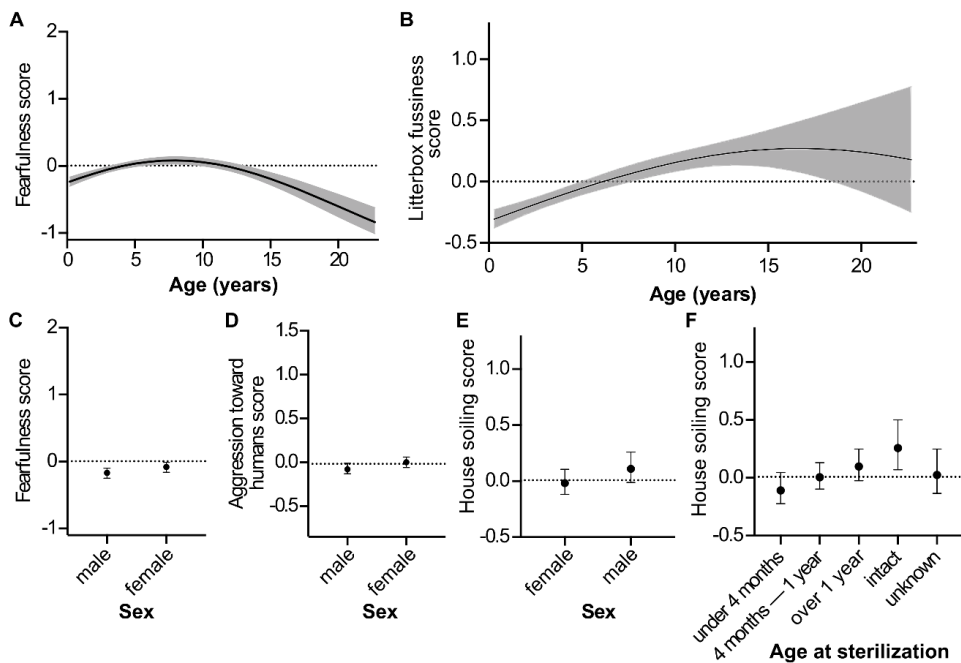
**Figure 7** Association of A) time since last vet visit with aggression toward humans, B) health problems with excessive grooming, and C) house soiling with urinary tract disease. Error bars indicate 95% confidence limits.  $N = 3255$  (A & B) and  $3036$  (C).

### 5.2.3 Demographic factors of behaviour

Age of the cat was associated with two of the behaviours. Cats around eight years of age had the highest score in fearfulness (Figure 8A) and the probability to exhibit litterbox fussiness increased with age (Figure 8B). No associations with aggression toward humans, excessive grooming, or house soiling were found.

Furthermore, sex of the cat was associated with three of the problematic behaviours, but no sex differences were found in excessive grooming or litterbox fussiness. Female cats had higher scores in fearfulness and aggression toward humans than males (Figures 8C and D), but males exhibited more house soiling than females (Figure 8E).

In addition, hormonal status of the cat was not associated with fearfulness, aggression, or excessive grooming (study II), but the age at sterilization was associated with house soiling (study III). Intact cats exhibited more house soiling than cats sterilized at under one year of age: the largest difference existed between intact cats and cats sterilized at under 4 months of age (Figure 8F). No difference was found between intact cats and cats sterilized later than this, or in litterbox fussiness.



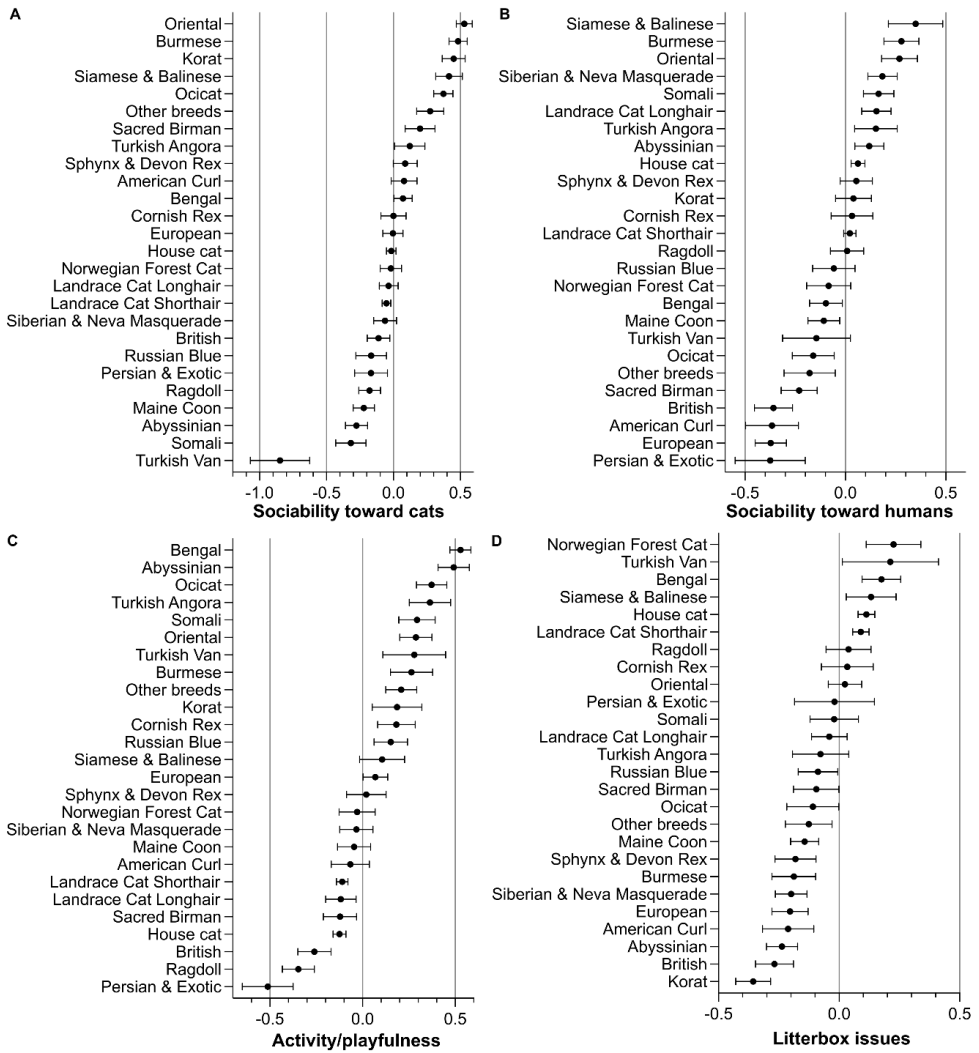
**Figure 8** Association of A) fearfulness and B) litterbox fussiness with age, C) fearfulness, D) aggression toward humans, and E) house soiling with sex of the cat, and F) house soiling with age at sterilization. Error bars and grey area indicate 95% confidence limits. N = 3255 (A, C & D), 3049 (B), and 3036 (E & F).

#### 5.2.4 Breed differences

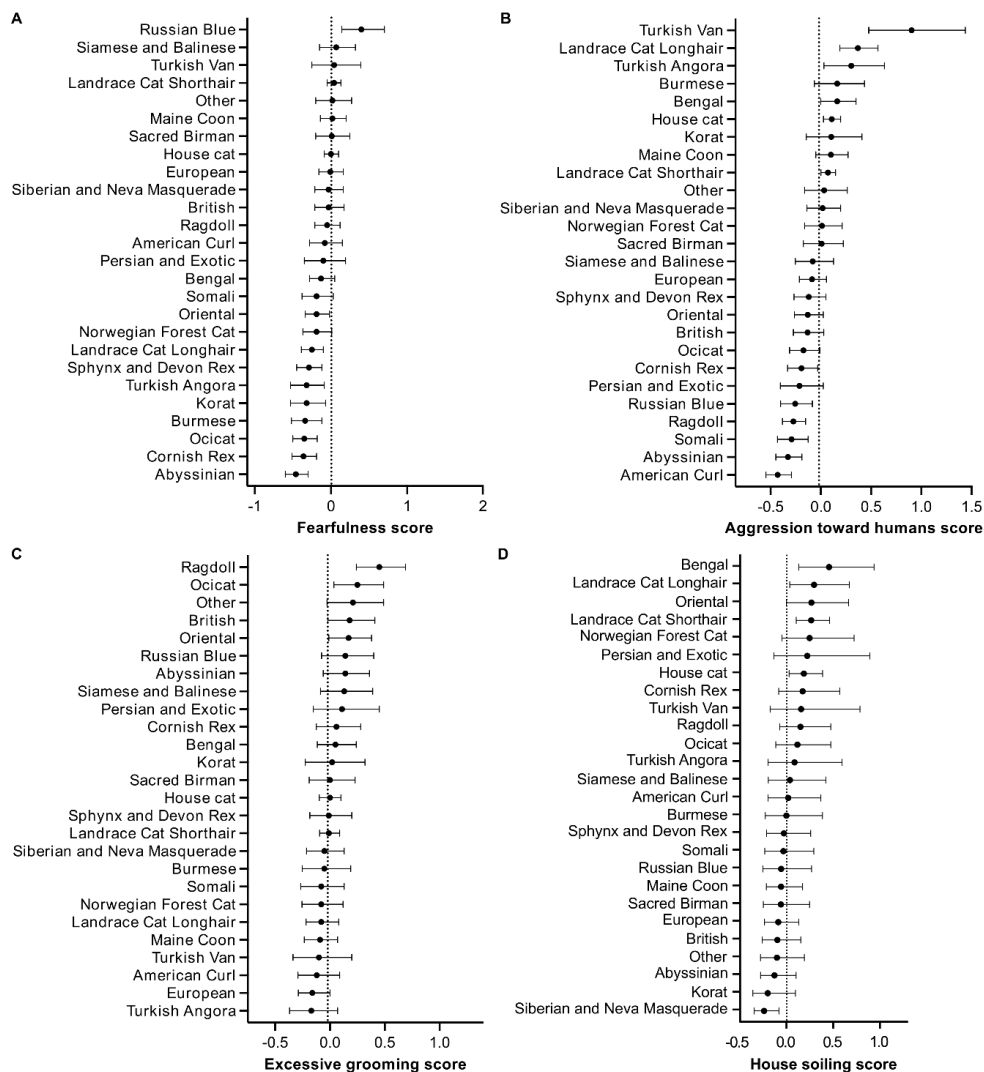
We found statistically significant differences between breed groups in all traits (study **I**). No other variables than the breed was taken into account in the personality and behaviour scores in the study **I**. The most social breeds toward other cats were Oriental, Burmese, and Korat (Figure 9A) and toward humans were Siamese & Balinese, Burmese, and Oriental (Figure 9B). Turkish Van was the least social breed toward other cats, and Persian & Exotic, European, American Curl, and British toward humans. The most active breeds were Bengal and Abyssinian, and the least active breeds were Persian & Exotic and Ragdoll (Figure 9C).

In the study **II** additional variables, such as the environmental variables, affected the cat's fearfulness, aggression toward humans, and excessive grooming scores. Therefore, the order of the breed groups is somewhat different between the studies **I** and **II** in those traits. In fearfulness, Russian Blue was the most fearful breed and Abyssinian the least fearful in both studies (Figure 10A, study **II**). Likewise, the Turkish Van was the most aggressive breed toward humans and American Curl the least aggressive in both studies (Figure 10B, study **II**). In contrast, Siamese & Balinese exhibited excessive grooming the most in the study **I**, but Ragdoll in the study **II** (Figure 10C, study **II**).

Breeds that exhibited the most litterbox issues in study **I** were Norwegian Forest cat, Turkish Van, and Bengal, and the least Korat (Figure 9D). In study **III**, where we formed two new litterbox issue factors, house soiling and litterbox fussiness, we found breed differences only in house soiling (Figure 10D). The breed scoring the highest in house soiling was Bengal and the lowest were Siberian and Neva Masquerade.



**Figure 9** Associations of the A) sociability toward cats, B) sociability toward humans, C) activity/playfulness, and D) litterbox issues with breed/breed group. Error bars indicate mean +/- se. N = 4316.



**Figure 10** Associations of the A) fearfulness, B) aggression toward humans, C) excessive grooming, and D) house soiling with breed/breed group, when also other variables have been taken into account. Error bars indicate 95% confidence limits. N = 3255 (A, B & C) and 3036 (D).

### 5.2.5 Importance of the variables

In the fearfulness model, the most important explanatory variable both relatively and absolutely, was sociability toward humans (Table 4). It also reached the suggested Cohen's cut-off value for a small effect size ( $f^2 = 0.02$ ) with the breed group variable (Cohen, 1988). In the aggression toward humans model, the most important variables, i.e., excessive grooming, sociability toward cats, and breed group, also reached small effect sizes together with the relatively less important

variable, fearfulness. In the excessive grooming model, the relatively most important variable, sociability toward humans, did not reach a small effect size, but aggression toward humans, litterbox issues, and breed group variables did. In the house soiling model, the relatively most important variable was sociability toward cats, and in the litterbox fussiness model, activity/playfulness. All variables in these two models failed to reach the cut-off for small effect size, but the one reaching the closest was the breed ( $f^2 = 0.019$ ). None of the variables in any models reached the suggested Cohen's cut-off values for medium ( $f^2 = 0.15$ ) or large ( $f^2 = 0.35$ ) effect sizes (Cohen, 1988).

**Table 4** Scaled variance-based variable importance (SV) and Cohen's  $f^2$  estimates of the variables explaining feline problematic behaviours. Cohen's  $f^2$  estimates that reached the suggested cut-off value for small effect size ( $f^2 = 0.02$ ) are bolded.

<b>Fearfulness</b>	<b>SV/<math>f^2</math></b>	<b>Aggression toward humans</b>	<b>SV/<math>f^2</math></b>	<b>Excessive grooming</b>	<b>SV/<math>f^2</math></b>
Sociability tow. humans	100/ <b>0.056</b>	Excessive grooming	100/ <b>0.04</b>	Sociability tow. humans	100/0.015
Age	69/0.014	Sociability tow. cats	99/ <b>0.036</b>	Aggression tow. humans	97/ <b>0.024</b>
Aggression tow. humans	53/0.012	Breed	87/ <b>0.054</b>	Litterbox issues	95/ <b>0.024</b>
Breed	44/ <b>0.033</b>	Sociability tow. humans	63/0.011	Age	63/0.001
Excessive grooming	43/0.007	Activity/playfulness	60/0.012	Fearfulness	60/0.009
Litterbox issues	33/0.014	Fearfulness	60/ <b>0.021</b>	Breed	60/ <b>0.021</b>
Main reason getting cat	22/0.018	Litterbox issues	38/0.01	Type of outdoor access	31/0.008
Socialization to humans	16/0.01	Age	24/0.001	Health problems	30/0.019
Acquisition place	16/0.009	Acquisition place	20/0.006	Sex	6/0.001
Type of outdoor access	14/0.017	Time since last vet visit	14/0.007		
Other cats in household	11/0.008	Other cats in household	10/0.004		
Sex	5/0.003	Sex	5/0.002		

<b>House soiling</b>	<b>SV/f<sup>2</sup></b>	<b>Litterbox fussiness</b>	<b>SV/f<sup>2</sup></b>
Sociability tow. cats	100/0.008	Activity/playfulness	100/0.015
Breed	82/0.019	Age	83/0.008
Fearfulness	58/0.005	Fearfulness	67/0.009
Age of sterilization	43/0.006	Children	24/0.007
Age	41/0.001	Sex	4/0.0002
Urinary track disease	38/0.009		
Playtime frequency	28/0.004		
Number of litterboxes	21/0.003		
Sex	15/0.003		

## 6 Discussion

This thesis examined the personality and problematic behaviour of a popular companion animal, the domestic cat. Large data utilized in these studies were collected with a self-designed, validated and reliability-tested survey, using citizen science, through cat owners participating in the research by answering the survey. The studies produced new knowledge for researchers, cat owners, breeders, and other people engaged with and interested in cats.

Study **I** inspected the structure of feline behaviour and personality, breed differences of over 26 breeds/breed groups and estimated the survey's reliability and validity with good results. Five personality and two behaviour traits were found; therefore the first hypothesis was met. Found personality traits, playfulness/activity, fearfulness, aggression, sociability toward humans, and sociability toward cats, parallel previous studies, corroborating the selected methodology. Two behavioural traits, litterbox issues and excessive grooming, are known problems in cats, demonstrating that the survey did not only catch differences in personality but also in behaviour. The valid and reliable survey used in the studies could be utilized in future studies, to help researchers to collect high-quality behavioural data. Breed profiles can guide prospective cat owners to the most suitable breeds for them, which can help to find their perfect cat.

Studies **II** and **III** examined the relationship of over 30 factors with common problematic traits in cats, i.e., fearfulness, aggression toward humans, excessive grooming, house soiling, and litterbox fussiness. Several demographic and environmental risk factors for the problems were found, thus, the second hypothesis was met. Associations of some of the factors, such as time since last vet visit, main reason for getting the cat, and children in a family with the problematic behaviours were never investigated before. In addition, several other factors, e.g., personality traits, socialization to humans and acquisition place, were examined only in a few previous studies. Thus, the results revealed many new associations, highlighting that personality greatly associates with problematic behaviours, especially fearfulness and both sociability traits. Finally, the findings partly replicated previous studies; the association between sex and fearfulness was found, for example. The findings additionally yielded new information to previously examined, but controversial subjects, such as the possible effects of hormonal status and the number of other cats in the household. The thesis

findings might help to prevent problematic behaviours or to treat them, and the findings can therefore be utilized by veterinarians as well as breeders and owners.

Compared to previous cross-sectional feline behaviour, personality, and risk factor studies, this thesis has some advantages. The survey and the structure of behaviour and personality were tested for validity and reliability more comprehensively than any other feline behaviour and personality study carried out previously. Moreover, the previous risk factor studies have mainly used univariate models or simplified multivariate models, which inadequately control for confounding factors, when analysing their data. Sample sizes were also larger than in most of the previous studies.

Even though the survey was tested for validity and reliability, the studies in this thesis have limitations. For example, some survey items may have been irrelevant for the cat behaviour, or on the other hand the list may have lack some relevant items for the cat behaviour, which have not been yet recognized by humans. The data used in the studies were based on an owner-completed survey, thus, the ratings were based on owners' perceptions that are subjective. The owners could have had, for example, an opinion on how the cat from a specific breed should behave, which is a source of bias. We also need acknowledged, that the interraters lived in the same household with the main raters, and therefore, were not independent. Even though, they were asked not to discuss about the survey items with the main raters, they have probably been discussing about the cat behaviour previously, which likely influenced their opinions. The method we used to test the survey's convergent validity is problematic as well as most of the studies we based our hypotheses on were not validated, and therefore could have been misleading. This was, however, the only available way to measure it at that time.

In addition, some information, such as the birthday of the cat, can have some inaccuracy as owners may have not known the exact day, influencing the age variable. The dataset was a convenience sample and thus, the study population may not represent the whole Finnish cat population. For example, not every person is eager or able to participate in internet-based surveys. Furthermore, health problems and diseases we studied were only based on the problems reported by the owners. Therefore, cats' health status was not evaluated by veterinarians and cats may have had some unreported health problems, which can affect the behaviour.

To utilize the information from the background and health sections statistically, we needed to simplify them in many cases. For example, originally numerical information of some variables was transformed into class variables, and we also had to combine certain categories together to reach reasonable group sizes. Despite this, the group size of Turkish Van breed was low in studies II and III (N = 34). Due to multicollinearity between some variables, e.g., hormonal status and age at sterilization, we had to drop some of them from the model selection process. In addition, some questions, such as the questions considering

the socialization period, had high missingness and we failed to use the information more precisely. The achieved results in studies **II** and **III** are associations rather than causations as the studies were cross-sectional. In the future, the causal effect of the identified factors should be studied with different study approaches, such as longitudinal and multidisciplinary methods, including combining genetics and microbiomics with behaviour ratings. Our studies included mainly Finnish cats, therefore, the findings may not be applicable to all cats globally, and the future studies should cover multiple countries with different cultures to see how generalized the findings are.

## **6.1 The structure of feline personality and behaviour**

We found seven personality and behaviour traits, which we named fearfulness, activity/playfulness, aggression toward humans, sociability toward humans, sociability toward cats, excessive grooming, and litterbox issues. Previous feline behaviour studies have not found the same exact structure for personality/behaviour, but many of them have found similar traits. The found fearfulness trait presents the boldness-shyness axis which is one of the most studied personality traits in animals (Réale et al., 2007). Previous studies have used, for example, the term shyness (Ahola et al., 2017; Salonen et al., 2019) or neuroticism (Arahoru et al., 2016, 2017; Litchfield et al., 2017) to describe a similar trait. Our activity/playfulness trait resembled traits previously named extraversion (Litchfield et al., 2017) and openness (Arahoru et al., 2016, 2017). A similar trait to aggression toward humans is sometimes named roughness (Arahoru et al., 2016, 2017). Previously used synonyms for sociability toward humans are human non-social (reverse-scored) (Ha & Ha, 2017), friendliness (Arahoru et al., 2016, 2017), and amiability (P. C. Bennett et al., 2017). Sociability toward cats parallel previously found traits cat social (Ha & Ha, 2017), aggression toward other cats (reverse-scored) (Ahola et al., 2017; Salonen et al., 2019), familiar cat aggression (reverse-scored) (Duffy et al., 2017), and dominance (reverse-scored) (Litchfield et al., 2017).

The last two traits, excessive grooming and litterbox issues can be considered more behavioural than personality traits, thus they have not been examined in most previous personality studies. Similar traits have only been reported in few previous personality and behavioural structure studies: in two other studies from the Finnish cat population (excessive grooming) (Ahola et al., 2017; Salonen et al., 2019) and in Fe-BARQ where litterbox issues were divided to factors named inappropriate elimination and elimination preferences. In Fe-BARQ (Duffy et al., 2017), on which our survey was mostly based on, the personality and behaviour structure consisted of 23 traits. When comparing their structure to ours, we can summarise that our individual traits included several of their traits, for example,

our fearfulness trait consisted mainly of the same statements as their sociability, stranger-directed aggression, and fear of novelty traits.

The results are highly dependent on the used methodology. For example, the data collection approaches and statistical methods used in the previous studies differ from each other and the studies in this thesis. For example, some studies used a principal component analysis instead of EFA (Ahola et al., 2017; Duffy et al., 2017; Salonen et al., 2019), a rotation (Arahorı et al., 2017; Duffy et al., 2017; Ha & Ha, 2017; Litchfield et al., 2017), or their items were adjectives instead of statements (Arahorı et al., 2017; Ha & Ha, 2017; Litchfield et al., 2017). Additionally, in Fe-BARQ the criticized Kaiser criterion (including all factors with eigenvalues > 1.0) (Howard, 2016; Preacher & MacCallum, 2003) was used to determine the number of extracted factors, compared to our study in which the scree test, parallel analysis, MAP test, and Goldberg's hierarchical tree were used to extract the optimal number of factors. These differences likely explain the remarkable difference in the extracted traits between our study and the Fe-BARQ. In conclusion, comparison between studies is somewhat difficult due to different methodologies. Despite the methodological differences, some traits were surprisingly similar compared to previous studies. Thus, it seems that the personality structure in cats includes at least the dimensions related to aggressiveness, fearfulness, and sociability.

## 6.2 Reliability and validity of the survey

Overall, the reliability and validity of the survey and factors were good. Internal consistency was acceptable, with a mean of 0.77, and most traits, excluding excessive grooming (0.66) and litterbox issues (0.60), reached the suggested cut-off value of 0.70 for Cronbach's alpha (Litwin, 2003; Tabachnick & Fidell, 2014). Cronbach's alpha is strongly affected by the length of the scale (Jones, 2008), and as these traits included only a few items, which is one possible explanation for lower values. Previous feline personality and behaviour studies have reported Cronbach's alpha values from 0.50 to 0.94 (Arahorı et al., 2016, 2017; P. C. Bennett et al., 2017; Duffy et al., 2017; Litchfield et al., 2017), and previous dog studies from 0.60 to over 0.90 (Salonen et al., 2021).

Inter-rater reliability was also good, as all traits exceeded the preferable cut-off value of 0.60 (Cicchetti, 1994), ranging from 0.61 to 0.87, with a mean of 0.72 ICC(1,1). We found only one previous feline personality study, which evaluated the inter-rater reliability with ICC: The inter-rater reliabilities of that study ranged from 0.31 to 0.55 ICC(3,1)(Gartner et al., 2014). In dog studies, the inter-rater reliability has ranged from 0.07 to 0.98 (Jakuba et al., 2013; Jones, 2008; Ley et al., 2009; Posluns et al., 2017; Salonen et al., 2021; Turcsán et al., 2018), and in human and animal personality studies, the mean interobserver agreement has been around 0.50 (Gosling, 2001).

Test-retest reliability was similarly good, as correlation between two timepoints ranged from 0.69 to 0.92, with a mean of 0.83. Correlations that exceed 0.70 indicate good test-retest reliability (Litwin, 2003). In one previous feline personality study, the test-retest reliability estimates varied between 0.63 and 0.76 (Arañuri et al., 2016). We found no other feline personality studies which had reported test-retest reliability, but in previous dog studies, the estimates have ranged between 0.70-0.94 (Jones, 2008; Salonen et al., 2021).

Interestingly, aggression toward humans had the lowest inter-rater reliability and the highest test-retest reliability. The low inter-rater reliability may indicate that family members do not handle the cat with equal frequencies, thus, some family members may avoid the situations where the cat usually behaves aggressively, e.g., during brushing. However, it is also possible that cats act differently toward different members of the family, allowing other members to handle them more than others. High test-retest reliability suggests that the trait is stable, thus, it can be considered part of the cat's personality. In contrast, excessive grooming had the highest inter-rater reliability and the lowest test-retest reliability. This opposite trend may indicate that the behaviour is easy to recognise when it happens, but that the behaviour is more periodic, and therefore not a stable personality trait but a behaviour trait.

The convergent validity of the survey was tested with 25 hypotheses, based mainly on previous studies. Only three of them were not met. We first hypothesized that males would have more litterbox issues than females (Hart & Hart, 2013b; Naderi et al., 2011; Strickler & Shull, 2013), and second that multicat households would have more litterbox issues than single-cat households (Barcelos et al., 2018). These previous studies had, however, studied only house soiling, and our litterbox issues trait also included aspects of substrate preference and cleanliness. The third unmet hypothesis addressed sociability toward humans, in which we hypothesized that cats with owner-reported problematic behaviour would have lower sociability toward humans than cats without reported behavioural problems (Duffy et al., 2017). As we met majority of our hypotheses, and the unmet ones were based only on a few previous studies, we can conclude that the convergent validity of our survey was good.

The discriminant validity of the survey was estimated by examining the correlations between factors. We found only one, previously non-reported negative correlation between sociability toward cats and aggression toward humans, indicating good discriminant validity. Although named to sociability toward cats, this trait included also items related to aggression toward cats and at least one previous study has found a correlation between aggression toward humans and cats (Salonen et al., 2019), which may explain this correlation.

Although the reliabilities of the factors were good, some of the individual items, such as “readily adapts to changes in environment or daily routines” and “growls or hisses when being brushed” were not that reliable. Those items were,

however, excluded before the final factor analysis. In the future, those statements should be deleted from the survey or reworded to make them clearer for the participants. In addition, the survey could be validated further with behavioural tests. As many previous studies lack validity and reliability measurement entirely or have used different reliability estimates the comparison of results is challenging. Summarizing, our survey is the most reliability and validity tested feline behaviour and personality survey currently available for the scientific researchers.

## **6.3 Factors associating with problematic behaviours**

### **6.3.1 Personality and behaviour traits & problematic behaviour**

We identified several factors associating with targeted behaviours, i.e., fearfulness, aggression, excessive grooming, house soiling, and litterbox fussiness (studies **II** and **III**). Fearfulness in particular was associated with other problematic behaviours, as fearful individuals were more aggressive and exhibited more often excessive grooming, house soiling, and litterbox fussiness. Similar correlations have been reported in previous studies (Ahola et al., 2017; Barcelos et al., 2018; Feaver et al., 1986; Normando et al., 2022; Porters et al., 2014). Aggressive behaviour caused by fear is a known phenomenon in cats (Amat & Manteca, 2019), which likely explains the first connection. For the rest of the connections, unmanageable stress can be a possible explanation. Both excessive grooming and litterbox issues can be induced by trauma or feeling stressed (Herron, 2010; Luescher, 2003; Nilson et al., 2022; Overall & Dunham, 2002), and we can hypothesize that fearful individuals might be more sensitive to change and other potential sources of stress, thus experiencing unmanageable stress or anxiety more often than non-fearful individuals.

Interestingly, high sociability toward humans was not only beneficial (study **II**). Highly human social cats were less fearful and less aggressive toward humans, which is found previously (Feaver et al., 1986), but they exhibited more excessive grooming than less human social cats. This result may suggest that highly human social cats are also more dependent on human company. Thus, highly social cats may feel more stress when separated from humans than less human sociable individuals. In fact, excessive grooming is one of the signs of separation-related problems in cats (de Souza Machado et al., 2020; Schwartz, 2002).

Other interesting behavioural comorbidities were that activity/playfulness correlated positively with aggression toward humans and litterbox fussiness. In cats, another common cause of aggression toward family members is misdirected predatory behaviour (Amat & Manteca, 2019), which may explain the connection between activity/playfulness and aggression. Therefore, these cats may benefit from additional stimulation, such as appropriate play, and the owner should avoid

playing roughly with the cat as it can increase the misdirected predatory behaviour (Amat & Manteca, 2019). Association with the litterbox fussiness was novel and required more research, but it may indicate that active cats use litterboxes more often, thus, the litterbox may need more frequent cleaning than the boxes of less active individuals. These founded behavioural comorbidities may be caused a shared genetical or neurological background between the traits, for example.

### **6.3.2 Early life socialization & other environmental factors contribute to problematic behaviour**

Many environmental and demographical factors were associated with cat behaviour and thus, we focus on only some of them in the Discussion: namely, early life conditions, social environment, health, age, sex, and hormonal status.

Early life conditions seem to be important for the cats' later personality, as poor socialization as a kitten and being a rescue cat associated with higher fearfulness. The socialization status of a large proportion of the rescue cats was unknown, although likely poor, as they usually have only little or not at all contact with humans before adoption. Few previous studies have investigated the effect of socialization on cat behaviour. These studies examined socialization in shelter- and laboratory-reared cats, but they similarly suggest that handling kittens during the early socialization period (0–12 weeks of age) is beneficial (Casey & Bradshaw, 2008b; Lowe & Bradshaw, 2002; McCune, 1995). In Finland, the majority of the purebred cat kittens leave the breeder and their mother and move to their new homes at the age of 14 weeks and thus, socialization should already start in the breeder's care. Based on our results, it seems that allowing the kittens to meet unfamiliar children and adults at least weekly is beneficial for the development of the kittens.

In addition, there was a significant difference between acquisition places as cats taken from breeders were more fearful than cats acquired from previous owners, which was a novel finding. However, the majority (~90%) of the pre-owned cats were missing the socialization to humans information. Without including other explanatory variables, pre-owned cats had a higher mean score in fearfulness than cats obtained from breeders. Cats obtained from previous owners were, however, more aggressive than cats acquired elsewhere. Aggressive behaviour is a common reason for relinquishing a cat (Salman et al., 2010), so aggressive behaviour could have been the reason for the previous owner searching for a new home for the cat. Acquisition place did not associate with excessive grooming, house soiling, or litterbox fussiness. Unlike in most countries, in Finland, selling cats in pet shops is illegal. Thus, this source of acquisition should also be considered in international studies.

Factors related to the current social environment, such as other cats, associated with problematic behaviours as well. As the ancestor of the cat, the African wildcat, is a solitary species, it is argued whether the cat enjoys the company of other cats or just tolerates them. In our studies, cats living alone or with only one other cat were more fearful than cats living with multiple cats. Similarly, Yamada and others (2020) found an association that group living may benefit fearful cats. This might indicate that cats feel safer in the company of (familiar) cats, as in a group, the detection of potential threats is more efficient. Another possibility is that fearful cats feel more confident around non-fearful cats, although this interaction is not yet tested. On the other hand, Menchetti and others (2018) noticed that the number of other cats correlated negatively with fearfulness (items: fearful), but positively with neuroticism (items: aggressive, shy, independent) score (Menchetti et al., 2018). Additionally, the found association may indicate that the owners of fearful cats may not want to take another cat, as they may think that the fearful cat would not cope with another cat, or it has been acquired from a multicat household as it could not cope there.

Furthermore, we discovered that cats living without conspecifics were slightly more aggressive toward humans than cats living with one or two other cats. There was not a significant difference compared to cats living with three or more conspecifics. This may indicate that having too many cats is not beneficial either, or that the category “three or more cats” is too diverse. Paralleling our results, several previous studies have reported less aggression toward human family members or humans in general in multi-cat households (Ahola et al., 2017; Amat et al., 2009; Amat & Manteca, 2019; Leech et al., 2022; Menor-Campos et al., 2021; Normando et al., 2022; Yamada et al., 2020). Menchetti and others (2018) also reported that sociability of the cat increased as the number of cats in the household did, but it is unsure if the interactions between cats increased just because the owner had more opportunities to witness those interactions (Menchetti et al., 2018). The presence of other cats enables interspecific communication and play, which likely are important for the majority of cats, thus preventing aggressive behaviour arising from frustration or misdirected predatory behaviour (Amat & Manteca, 2019). On the other hand, the associations we found can indicate that the owners of fearful or aggressive cats may be unwilling to obtain more cats, as they predict that the situation may worsen. Indeed, a previous study noticed that getting more cats increased the probability of aggressive behaviour between the cats (Elzerman et al., 2020), thus taking more cats can either increase or decrease the overall welfare depending on the cat.

Interestingly, we found no associations between house soiling or litterbox fussiness and the number of other cats in the household, unlike some previous studies (Barcelos et al., 2018; Duffy et al., 2017; Pryor et al., 2001). One possible reason for the absence of this association might be that we could not separate marking and latrine behaviours from each other. However, we found that

sociability toward cats associated negatively with house soiling, which likely is a more important factor in our study than the number of other cats in the household. Thus, the welfare of an unsocial cat might decrease from living in a multicat-household, which might be seen as more prevalent house soiling events.

In addition to the number of other cats, the possible effect of dogs and children on litterbox issues were investigated in study **III**. We found that in families with children, cats exhibited more litterbox fussiness, but dogs did not associate with the problems. Children are a known stressor for cats, as they might pursue cats (Herron, 2010), for example. Additionally, in the household with children, the owners may clean the litterboxes less often as the children keep them occupied. Furthermore, in a previous study, owners with children had less anxious attachment toward their cats than childless owners (Ståhl et al., 2023). This may affect the quality of the care the cat receives, as more anxiously attached owners may be more concerned about their cat's welfare and therefore monitor the cat's behaviour and environmental quality more consistently.

Healthcare associated with problematic behaviours as well. Cats that had last seen a veterinarian over two years ago or never were more aggressive than cats that had visited a veterinarian less than one year ago. Thus, it is possible that aggressive behaviour in some of the cats could be caused by an undiagnosed health problem or pain, which are possible reasons for aggressive behaviour in cats (Amat & Manteca, 2019; Mills et al., 2020). As the recognition of pain in cats is challenging, especially for non-professionals (Monteiro et al., 2023), such as common cat owners, yearly health checks by a professional are recommended (Vogt et al., 2010). On the other hand, owners of aggressive cats may avoid visits to a veterinarian as they know their cat will behave aggressively (Karn-Buehler & Kuhne, 2021) and thus, avoid these uncomfortable situations.

Health problems may cause or increase excessive grooming and house soiling. Existence of one or more owner-reported health problems associated with excessive grooming. This is not surprising as excessive grooming can be a sign of numerous health problems (Beale, 2012; Tilley & Smith, 2016), which is more common than excessive grooming caused purely by compulsion. In study **III**, the history of having a urinary tract disease associated with higher house soiling, replicating the results of Horwitz (1997)(Horwitz, 1997). Surprisingly, the other studied disease groups, i.e., diseases causing excessive drinking, intestinal disorders, and musculoskeletal diseases did not associate with litterbox problems. Not many previous studies have examined the effect of specific disease groups on a large scale, because cats with health problems are usually excluded or their diseases are treated before the actual comparison between the test and control groups. One study that included disease-related factors did not find statistically significant associations (N = 245) (Barcelos et al., 2018), but another study found that having any health problem associated with house soiling (P-value < 0.001, N

= 6096) (Normando et al., 2022). Thus, we argue that the prevalences of studied problematic behaviours could be decreased by enhanced healthcare.

Age associated only with two of the problems, fearfulness, and litterbox fussiness. The association with fearfulness was non-linear: cats around nine years of age were the most fearful, and cats younger or older than this were less fearful. Previous literature has reported that younger cats were less fearful than older ones (Ahola et al., 2017; Yamada et al., 2020). Previous studies have reported that older cats are also more aggressive toward strangers and other cats (Ahola et al., 2017), thus, we expected to find an association between age and aggression toward humans as well, but this was not the case. In addition, older cats exhibited more litterbox fussiness than younger cats. It is possible that they have learned to associate certain substrate types with negative experiences, such as pain during urination, and as they have lived longer have had more opportunities to develop some problems such as fussiness. However, we expected to find them to be more prone to house soiling as well, as previous studies have reported older individuals exhibiting it more (Duffy et al., 2017; Normando et al., 2022). Moreover, the real effect of aging on problematic behaviour can be tricky to study as the problematic individuals could have been euthanised at a young age. Thus, there should be proportionally more old problematic individuals than can be seen in the studies, and this can bias the results.

Sex of the cat associated with three problematic behaviours: fearfulness, aggression toward humans, and house soiling. Males were less fearful and less aggressive than females. This result disagrees with some of the studies (Lee et al., 2007; Menchetti et al., 2018; Naderi et al., 2011; Tamimi et al., 2015), and agrees with others (Ahola et al., 2017; Arahori et al., 2017; Wassink-van der Schot et al., 2016; Yamada et al., 2020). Moreover, male cats exhibited more house soiling than female cats, which parallels with previous literature (Hart & Hart, 2013b; Pryor et al., 2001; Strickler & Shull, 2013). In free-ranging cat populations, both males and females urine mark, but males do it more often (Feldman, 1994), which may explain this connection.

Interestingly, we did not find hormonal status to associate with any of the problems excluding house soiling, as previous studies have found sterilized cats to be more aggressive and fearful toward strangers than intact cats (Ahola et al., 2017; Arahori et al., 2017). In contrast, in a free-ranging population, the cats became less aggressive after the sterilization in the absence of resources such as shelter and food, but their aggressivity did not change in the presence of them (Cafazzo et al., 2019). Previous literature about the subject is, however, scarce, maybe because of the high number of sterilized cats. In our studies, the proportion of sterilized cats was 70% and 90% when also including cats that were administered medical contraception.

However, in house soiling the onset of sterilization mattered. Cats sterilized later than one year old or not at all exhibited more house soiling than cats

sterilized earlier than this. Previously, sterilization has been used successfully to reduce or prevent urine marking in free-roaming cats (Cafazzo et al., 2019). Also, another study reported that cats sterilized before 5.5 months of age had less marking behaviour than cats sterilized at an older age (Spain et al., 2004). However, a third study which compared cats sterilized at age 8 to 12 weeks to those sterilized at 6 to 8 months did not find any difference between them (Porters et al., 2014). Thus, it seems that sterilization before adulthood may reduce house soiling, at least if it is motivated by marking behaviour.

### **6.3.3 Breeds differ in their behaviour & personality**

Breed was significantly associated with every studied trait except litterbox fussiness. We examined breed differences in study **I** without taking the effects of other possible variables into account. In studies **II** and **III**, we used more complicated models to explain the studied traits, therefore including also other variables, which affected the breeds' mean values. However, when comparing the orders of the breeds between studies **I**, **II**, and **III**, they remained quite similar. The largest difference that was observed when taking other variables into account, was that the differences between the breeds in the traits' extreme ends were smaller in studies **II** and **III** than in study **I**. In general, most of the breeds did not differ statistically in a pairwise comparisons, and the individual differences within a breed were large (studies **II** and **III**).

The most active/playful breeds were Bengal and Abyssinian, and the least active breeds were Persian and Exotic, Ragdoll and British. This replicates the results of some previous studies (Duffy et al., 2017; Salonen et al., 2019; Takeuchi & Mori, 2009). In addition, Bengal showed the most predatory behaviour and Persian the least in the study of Wilhelmy and others (2016)(Wilhelmy et al., 2016). Bengal is a relatively new hybrid cat breed (*Felis silvestris catus* x *Prionailurus bengalensis*) (Martos Martinez-Caja et al., 2021) and the "wild" heritage may still affect their behaviour, i.e., activity level. However, Martos Martinez-Caja and others (2021) did not find significant differences between Bengals from generations F1-F4 and F5 or later (Martos Martinez-Caja et al., 2021). The least active breed group, Persian and Exotic, on the other hand, are brachycephalic breeds. Brachycephalic breeds suffer from breathing issues more often than non-brachycephalic ones (Farnworth et al., 2016). Problems related to breathing have been associated with lower activity (Farnworth et al., 2016), which might suggest that cats with breathing problems avoid unnecessary moving and therefore are less active.

Some traits were not studied further in the studies **II** and **III**: sociability toward cats and sociability toward humans. Oriental shorthair and longhair, Burmese, and Korat were the most social breeds toward cats and the Siamese and Balinese, Burmese and Oriental the most social breeds toward humans. Previous

studies have reported that Oriental breeds and Abyssinians show aggression toward other cats more likely than other breeds (Takeuchi & Mori, 2009; Wilhelmy et al., 2016), thus these results differ from previous studies. However, they greatly parallel the results of a previous study on the Finnish cat population (Salonen et al., 2019), and in general, Oriental breeds have been perceived as highly human depended and social.

Russian Blue was the most fearful breed in both studies (studies **I** and **II**). Similarly, Russian Blues have had the highest probability of shyness toward strangers and nervousness in two previous studies (Salonen et al., 2019; Takeuchi & Mori, 2009). Moreover, Turkish Van exhibited the most aggression toward humans in both studies. This breed has also been ranked as the most aggressive breed in previous studies from the local cat population (Salonen et al., 2019; Vapalahti et al., 2016), but this breed has not been included in comparative behaviour studies outside of Finland. Therefore, it is unknown whether this trait exists only in the Finnish Turkish Van population or whether it is a global challenge. In dogs, there is evidence that same breeds differ regionally from each other in their behaviour (Wan et al., 2009), but it is not known if the differences arise from cultural differences or genetic differences. This may also be true with cat breeds. However, the sample sizes of Turkish Van in studies **I** and **II** are very small ( $N = 34$  &  $44$ ), so the results might be somewhat biased.

The breeds that exhibited the most excessive grooming in study **I** were Siamese/Balinese and Ragdoll. Similarly, Ragdoll showed this behaviour the most in study **II**, but the average score of Siamese and Balinese was close to the average of all cats. Usually, Siamese and Balinese are grouped into the same breed group with Oriental short- and longhair, forming a group named “Oriental breeds”. Although Oriental breeds showed a high probability of excessive grooming also in a previous study from the local cat population (Salonen et al., 2019), the order of the rest of the breeds is different. Interestingly, another study did not find a difference in excessive grooming between Oriental breeds and other included breeds (Wilhelmy et al., 2016). Thus, it seems that other factors are more important in excessive grooming than the breed of the cat.

Furthermore, the association between feline litterbox issues and the breed was investigated in the studies **I** and **III**. In the study **I**, the litterbox issues trait included aspects of house soiling as well as substrate preference and cleanliness. In the study **III**, the studied traits were house soiling and litterbox fussiness, but we did not find breed differences in the latter. The breeds exhibiting the most litterbox issues in the study **I** were Norwegian Forest cat, Turkish Van, and Bengal. Bengal also exhibited most house soiling in the study **III**, followed by breeds such as the landrace cat, Oriental, Norwegian Forest cat, and Persian and Exotic. Similarly, previous studies have found similarly Bengal (Wilhelmy et al., 2016) and Persian (Amat et al., 2009; Wassink-van der Schot et al., 2016) to be

more prone to house soiling. In contrast, some previous studies did not report breed differences in this trait at all (Naderi et al., 2011; Takeuchi & Mori, 2009).

The most prevalent breed in our data was the landrace cat, which we divided into short- and longhaired cats. Even though both are born to the same litters, we found differences in personalities between the short- and longhaired landrace cats. Interestingly, longhaired cats exhibited more aggression toward humans and were less fearful than shorthaired cats. We can only hypothesize reasons for this difference. Longhaired cats are more likely to develop tangles and brushing them out can be painful to the cat, thus, causing more frequent situations to show aggressive behaviour. Additionally, there could be a genetic link between genes affecting fur length and genes affecting behaviour in landrace cats.

In summary, although previous studies have different breed compositions, the results were similar for the breeds present in all studies (Amat et al., 2009; Duffy et al., 2017; Hart & Hart, 2013b; Salonen et al., 2019; Takeuchi & Mori, 2009; Tamimi et al., 2015; Wilhelmy et al., 2016). The existing breed differences may indicate a genetic component underlying differences in personality, but owners can also have assumptions about the breed's behaviour and personality, which may bring bias to the results. In addition, the body language of some breeds, such as the tailless Manx, and lop-eared Scottish Fold, might be harder to interpret. Thus, further genetic research is needed to investigate the relationship of breed with behaviour and personality.

## 6.4 Importance of factors

The importance of breed/breed group for personality and behaviour traits was trait specific, as its relative and absolute importance were high in fearfulness and aggression toward humans, but lower in excessive grooming and house soiling. However, breed group reached at best, a small effect size according to the  $f^2$  cut-offs (small = 0.02, medium = 0.15, large = 0.35) suggested by Cohen (1988) (Cohen, 1988). A recent dog study (Salonen et al., 2023), which used a similar methodology, reported that breed reached a small effect size in many personality traits as well, including insecurity, which parallels fearfulness, and in aggressiveness/dominance.

The strict following of Cohen's  $f^2$  cut-offs can be, however, misleading as personality traits often yield only small effect sizes, even though their effects are cumulative and thus more important in the long-term than their effect size may indicate (Funder & Ozer, 2019). According to Funder and Ozer (2019), the estimates should only be compared with other well-understood findings (so-called benchmarks), and not with arbitrary cut-offs. They also suggest that the researchers should stop using the labels small, medium, and large (Funder & Ozer, 2019).

Nevertheless, we additionally decided to compare our results with the correlation cut-offs developed for individual differences researchers (small = 0.10, medium = 0.20, large = 0.30) by Gignac and Szodorai (2016). Those cut-offs are based on 87 meta-analyses from personality/individual difference publications (Gignac & Szodorai, 2016), and they correspond to the Cohen's  $f^2$  cut-offs 0.02, 0.05, and 0.10, respectively (Cohen, 1988; Salonen et al., 2023). According to these cut-offs, the breed reached small effect sizes in fearfulness and excessive grooming, and medium in aggression toward humans.

Personality traits were relatively the most important factors in all studied traits. Sociability toward humans was the most important trait in fearfulness and excessive grooming, and sociability toward cats in aggression and house soiling. In fearfulness, sociability toward humans reached a medium effect size, and in aggression, sociability toward cats a small effect size (according to newly suggested cut-offs). Activity/playfulness was relatively important both in aggression and litterbox fussiness but did not reach the cut-off for small effect size. In addition, fearfulness and excessive grooming reached small effect sizes in aggression.

Age was relatively the second most important factor in fearfulness and litterbox fussiness, and the fourth in excessive grooming. Similarly, age was among the most important factors explaining insecurity in the dog study of Salonen and others (2023), but also in aggressiveness/dominance. However, they did not study the effect of other personality traits. When considering only non-personality traits, age was likewise the second most important factor in aggression toward humans in our study. Age of sterilization had relatively mediocre importance for house soiling. Neither age nor sterilization reached any of the suggested effect size cut-offs. Moreover, the importance of sex was low. These results parallel the results of a dog study of Salonen and others (2023). In addition, both relative and absolute importance of the remaining factors, i.e., health, owner, environmental, and demographic factors were low.

We did not expect that any factors would explain a large portion of the variance in problematic behaviours as they are known to be extremely complex. Previous cat studies have not reported effect sizes but based on our studies it seems that the most important factors for problematic behaviours are the cat's breed and personality traits, especially fearfulness and sociability.

## 7 Conclusions

The research field of companion animal behaviour and personality is an important but complex subject. In companion animals, problematic behaviour is a common welfare issue. This doctoral thesis sheds light on the personality and problematic behaviours of the domestic cat by examining the associations of multiple factors with selected problems simultaneously. The focused problems in this thesis were fearfulness, aggression toward humans, excessive grooming, and litterbox issues (house soiling and litterbox fussiness). The studied explanatory variables included factors related to personality, behaviour, early life conditions, current environment, health, demographics, and genetics (breed), covering a wide range of possible underlying factors.

Feline personality divided into five personality traits and two additional behaviour traits. The personality dimensions fearfulness-boldness, sociability-aggression, and activity-calm have been found previously in the cat and other species, thus, the found structure shows great similarity with previous findings. Especially, fearfulness is a trait that is very often studied and found in a diverse spectrum of animal species. This may indicate that the fundamentals building blocks of behaviour are similar throughout the animal kingdom.

This thesis utilized a large dataset, which was collected with an owner-completed survey. Surveys are a common but debated method to collect behavioural data as they can be subjective. Most of the survey studies still lack the estimation for reliability and validity entirely. This is a concerning phenomenon as unreliable data will yield unreliable results, which can lead to ineffective attempts to solve problematic behaviours. Thus, testing the reliability and validity of the survey comprehensively was a fundamental step for this thesis. Both reliability and validity estimates were good and justified the further use of the data. Furthermore, the validated survey could be utilized in future studies in different cat populations.

Personality traits had the most important roles in problematic behaviours. Fearfulness, in particular, seemed to be a remarkable personality trait that was positively associated with all the other problematic behaviours. In addition, being sociable was beneficially associated with most of the problems but increased the probability to exhibit excessive grooming. Comorbidity between personality traits was common, which is in line with previous studies. These findings suggest that

personality traits are interconnected. The mechanism can be, for example, genetic or neurologic, but the pathway cannot be solved based on this thesis.

Breeds showed notable differences in their personality, and some breeds exhibited specific problematic behaviours more frequently than others. Different cat breeds differ genetically from each other, thus existing breed differences give more evidence for the inheritance of personality and behaviour traits. The heritability of the problematic behaviours could indicate that their incidence could be lowered in the cat population by making careful breeding choices, which emphasises the importance of the breeding individuals' personalities.

Demographic factors, such as sex and age, seemed to be less important risk factors for problematic behaviours but the results suggest that sterilization before the age of one year may reduce the probability of house soiling. Female cats exhibited more fearfulness and aggression, but less house soiling than males, which agrees with most of the previous literature. Also, human and dog females tend to be more fearful and anxious than males, suggesting similar effects of sex hormones in all these mammals. Furthermore, cats around eight years old were the most fearful, which mainly agrees with the previous findings. Also in other species, young animals tend to be more curious and less fearful than adult individuals. Moreover, very old individuals tend to be calmer, maybe because not many experiences are novel to them anymore, or because their movements are restricted because of health problems or energy-saving strategies.

Numerous environmental factors were associated with the studied problems, but their individual effects were smaller than the effects of personality or breed. However, the results suggested that proper socialization as a kitten may decrease fearfulness and having multiple cats may help to reduce fearfulness and aggression. Based on these results, it seems that the social environment is important during the development of the kitten as well as in adulthood. Moreover, health issues associated with excessive grooming and house soiling, and a long time since the last vet visit with aggression toward humans, reflect that they all can be signs of health problems instead of being solely behavioural in origin. Thus, proper health care, such as annual visits to a veterinarian, could help avoid these problems. In conclusion, even though it seems that endogenous traits (personality and genetics) play a big role in the development of problematic behaviours, environmental factors also have an important role in the phenomena.

In summary, this thesis revealed new associations behind the domestic cat's problematic behaviours and replicated some previous ones. Some factors, such as fearfulness, were associated with more than one problem and others were problem-specific. The factors' effect sizes were small in all problem behaviours, which reflects the complex background of behaviour. Identification of the predisposing factors enables changes in the rearing of cats' and their current environments, which may potentially prevent and treat problematic behaviour. This could increase the welfare of both cats and their owners. However, as the

studies of this thesis were cross-sectional, further longitudinal or prospective controlled studies with international samples are needed to reveal the causality and appropriateness of our findings.

# Acknowledgements

This doctoral thesis was conducted at the University of Helsinki, Department of Veterinary Biosciences, Faculty of Veterinary Medicine; Department of Medical and Clinical Genetics, Faculty of Medicine; and Folkhälsan Research Center.

This thesis was carried out as a doctoral student in the Doctoral Programme in Clinical Veterinary Medicine (CVM). The studies in this thesis were financially supported by a Finnish cat association Suomen Kissaliitto ry, the Agria and Svenska Kennel Club Research Fund, the Academy of Finland, Kinship Partners Inc, and the Doctoral Programme in Clinical Veterinary Medicine.

First, I want to thank my all three supervisors Hannes Lohi, Anna-Maija Virtala, and Milla Salonen. Thank you, Hannes, for this opportunity to be part of your research group. Anna-Maija, I thank you for accepting Hannes's unexpected phone-invitation to become one of my supervisors. Your comments and insights outside of our research group were priceless. Milla, we can say that you initiated my PhD journey by introducing me to Hannes. As you may already know, you are not only the best colleague and supervisor that I could have, but also a great, supportive, and important long-term friend for me.

I am warmly grateful to our cat expert panel, Kirsi Juuti, Kati Pulli, Miira Hellsten, Jaana Pohjola, Ann-Marie Määttä, Carin Sahlberg, Pirjo Tomperi, Arja Martikainen, and Inkeri Siltala for their suggestions and comments regarding the survey. Likewise, I am grateful to all cat owners participating in the study, and to cat and cat breed organizations for advertising the survey.

I want to thank all employees of Petsofi Ltd. for helping us with data collection and for designing together feline personality reports for the survey participants.

Thank you, Suvi Ruuskanen and Anna Valros, for being my thesis committee members and watching over my PhD journey. Similarly, I am grateful to Docent Sonja Koski and Associate Professor Lee Niel for the review of my thesis and for your valuable feedback which helped me to improve my work.

I am extremely grateful to my all co-authors in publications in- and outside of this thesis. Thank you, Milla, Jenni Puurunen, Emma Hakanen, and Sini Sulkama for all the discussions and constructive company. César Araujo, a special thank go to you for helping with the data collection and management.

I am very happy to have conducted my thesis in this thesis group with so many inspirational past and current members. So, thank you, César, Milla, Jenni, Emma, Sini S., Ileana, Inka, Julia, Lea, Maria, Marjo, Meharji, Riika, Sini K.,

Sruthi, Tiina, Sara, Aada and others for all the great discussion we had, both related and unrelated to the work. Sini K., thank you for taking care of the plants when I was unable to come to the office. Julia, your programming skills were a great help in the model selection process.

Finally, I want to thank my family and friends. I am deeply grateful to my mother and my grandmother, who unfortunately did not see the completion of my thesis. You were always there to encourage me. Dear friends, thank you for offering me non-academic entertainment and company, which let me take brief breaks from a hectic academic world. Joni, I am deeply grateful for your unending support during all these years. Pyry, thank you for joining me at the final steps of my journey. Last, I want to thank past and current furry members of my family, Santtu, Sirius, Unski, Tiuku, and Tatjana with whom I have been honoured to share a part of my life.

## References

- Ahola, M. K., Vapalahti, K., & Lohi, H. (2017). Early weaning increases aggression and stereotypic behaviour in cats. *Scientific Reports*, *7*(1), 10412. <https://doi.org/10.1038/s41598-017-11173-5>
- Amat, M., Camps, T., & Manteca, X. (2016). Stress in owned cats: behavioural changes and welfare implications. *Journal of Feline Medicine and Surgery*, *18*(8), 577–586. <https://doi.org/10.1177/1098612X15590867>
- Amat, M., de la Torre, J. L. R., Fatjó, J., Mariotti, V. M., Van Wijk, S., & Manteca, X. (2009). Potential risk factors associated with feline behaviour problems. *Applied Animal Behaviour Science*, *121*(2), 134–139. <https://doi.org/10.1016/j.applanim.2009.09.012>
- Amat, M., & Manteca, X. (2019). Common feline problem behaviours: Owner-directed aggression. *Journal of Feline Medicine and Surgery*, *21*(3), 245–255. <https://doi.org/10.1177/1098612X19831206>
- Amat, M., Manteca, X., Brech, S. Le, Ruiz de la Torre, J. L., Mariotti, V. M., & Fatjó, J. (2008). Evaluation of inciting causes, alternative targets, and risk factors associated with redirected aggression in cats. *Journal of the American Veterinary Medical Association*, *233*(4), 586–589. <https://doi.org/10.2460/javma.233.4.586>
- Arahoru, M., Chijiwa, H., Takagi, S., Bucher, B., Abe, H., Inoue-Murayama, M., & Fujita, K. (2017). Microsatellite polymorphisms adjacent to the oxytocin receptor gene in domestic cats: association with personality? *Frontiers in Psychology*, *8*(DEC), 2165. <https://doi.org/10.3389/fpsyg.2017.02165>
- Arahoru, M., Hori, Y., Saito, A., Chijiwa, H., Takagi, S., Ito, Y., Watanabe, A., Inoue-Murayama, M., & Fujita, K. (2016). The oxytocin receptor gene (OXTR) polymorphism in cats (*Felis catus*) is associated with “Roughness” assessed by owners. *Journal of Veterinary Behavior*, *11*, 109–112. <https://doi.org/10.1016/j.jveb.2015.07.039>
- Bamberger, M., & Houpt, K. A. (2006). Signalment factors, comorbidity, and trends in behavior diagnoses in cats: 736 cases (1991–2001). *Journal of the American Veterinary Medical Association*, *229*(10), 1602–1606. <https://doi.org/10.2460/JAVMA.229.10.1602>
- Barcelos, A. M., McPeake, K., Affenzeller, N., & Mills, D. S. (2018). Common risk factors for urinary house soiling (periuria) in cats and its differentiation: the sensitivity and specificity of common diagnostic signs. *Frontiers in Veterinary Science*, *5*(108), 1–12. <https://doi.org/10.3389/fvets.2018.00108>
- Bateson, M., & Martin, P. (2021). *Measuring Behaviour: An Introductory Guide* (4th ed.). Cambridge University Press. <https://doi.org/10.1017/9781108776462>
- Beale, K. (2012). Feline demodicosis: A consideration in the itchy or overgrooming cat. *Journal of Feline Medicine and Surgery*, *14*(3), 209–213. <https://doi.org/10.1177/1098612X12439268>

- Ben-Shachar, M., Lüdtke, D., & Makowski, D. (2020). effectsize: estimation of effect size indices and standardized parameters. *Journal of Open Source Software*, 5(56), 2815. <https://doi.org/10.21105/joss.02815>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society*, 57(1), 289–300. <https://www.jstor.org/stable/2346101>
- Bennett, P. C., Rutter, N. J., Woodhead, J. K., & Howell, T. J. (2017). Assessment of domestic cat personality, as perceived by 416 owners, suggests six dimensions. *Behavioural Processes*, 141, 273–283. <https://doi.org/10.1016/j.beproc.2017.02.020>
- Bennett, S. L., & Khan, M. Z. (2021). Managing compulsive disorders in cats. *Today's Veterinary Practice*, September/October 2021, 98–102. <https://todaysveterinarypractice.com/behavior/managing-compulsive-disorders-in-cats/>
- Bernstein, I. S., Gordon, T. P., & Rose, R. M. (1983). The interaction of hormones, behavior, and social context in nonhuman primates. In B. B. Svare (Ed.), *Hormones and Aggressive Behavior* (pp. 535–561). Springer US. [https://doi.org/10.1007/978-1-4613-3521-4\\_20](https://doi.org/10.1007/978-1-4613-3521-4_20)
- Bleidorn, W., Schwaba, T., Zheng, A., Hopwood, C. J., Sosa, S. S., Roberts, B. W., & Briley, D. A. (2022). Personality stability and change: A meta-analysis of longitudinal studies. *Psychological Bulletin*, 148(7–8), 588–619. <https://doi.org/10.1037/bul0000365>
- Bradshaw, J. (2018). Normal feline behaviour: ... and why problem behaviours develop. *Journal of Feline Medicine and Surgery*, 20(5), 411–421. <https://doi.org/10.1177/1098612X18771203>
- Bradshaw, J. W. S., Neville, P. F., & Sawyer, D. (1997). Factors affecting pica in the domestic cat. *Applied Animal Behaviour Science*, 52, 373–379. [https://doi.org/10.1016/S0168-1591\(96\)01136-7](https://doi.org/10.1016/S0168-1591(96)01136-7)
- Briffa, M., & Greenaway, J. (2011). High in Situ repeatability of behaviour indicates animal personality in the beadlet anemone *Actinia equina* (Cnidaria). *PLoS ONE*, 6(7), e21963. <https://doi.org/10.1371/journal.pone.0021963>
- Burn, C. C. (2011). A vicious cycle: A cross-sectional study of canine tail-chasing and human responses to it, using a free video-sharing website. *PLoS ONE*, 6(11), e26553. <https://doi.org/10.1371/journal.pone.0026553>
- Cafazzo, S., Bonanni, R., & Natoli, E. (2019). Neutering effects on social behaviour of urban unowned free-roaming domestic cats. *Animals*, 9(12), 1105. <https://doi.org/10.3390/ani9121105>
- Canty, A., & Ripley, B. (2021). *boot: bootstrap R (S-Plus) functions*. <https://cran.r-project.org/web/packages/boot/index.html>
- Carere, C., & Maestripieri, D. (2013). Animal Personalities: Who cares and why? In C. Carere & D. Maestripieri (Eds.), *Animal Personalities. Behaviour, physiology and evolution* (pp. 1–25). University of Chicago Press. <http://bibliovault.org/BV.landing.epl?ISBN=9780226921976>
- Carney, H. C., Sadek, T. P., Curtis, T. M., Halls, V., Heath, S., Hutchison, P., Mundschenk, K., & Westropp, J. L. (2014). AAFP and ISFM guidelines for diagnosing and solving house-soiling behavior in cats. *Journal of Feline Medicine and Surgery*, 16(7), 579–598. <https://doi.org/10.1177/1098612X14539092>
- Casey, R. A., & Bradshaw, J. W. S. (2008a). Owner compliance and clinical outcome measures for domestic cats undergoing clinical behavior therapy.

- Journal of Veterinary Behavior*, 3(3), 114–124.  
<https://doi.org/10.1016/j.jveb.2008.02.001>
- Casey, R. A., & Bradshaw, J. W. S. (2008b). The effects of additional socialisation for kittens in a rescue centre on their behaviour and suitability as a pet. *Applied Animal Behaviour Science*, 114(1–2), 196–205.  
<https://doi.org/10.1016/j.applanim.2008.01.003>
- Cicchetti, D. V. (1994). Guidelines, criteria, and rules of thumb for evaluating normed and standardized assessment instruments in psychology. *Psychological Assessment*, 6(4), 284–290. <https://doi.org/10.1037/1040-3590.6.4.284>
- Cohen, J. (1988). *Statistical Power Analysis for the Behavioral Sciences* (2nd ed.). Lawrence Erlbaum Associates.  
<https://doi.org/10.4324/9780203771587>
- Cordonnier, M., Perrot, A., Ferry, N., Bonnaud, E., & Baudry, E. (2023). Pet cat personality linked to owner-reported predation frequency. *Ecology and Evolution*, 13, e9651. <https://doi.org/10.1002/ECE3.9651>
- de Souza Machado, D., Oliveira, P. M. B., Machado, J. C., Ceballos, M. C., & Sant'Anna, A. C. (2020). Identification of separation-related problems in domestic cats: a questionnaire survey. *PLOS ONE*, 15(4), e0230999.  
<https://doi.org/10.1371/journal.pone.0230999>
- Delgado, M. M., Munera, J. D., & Reevy, G. M. (2012). Human perceptions of coat color as an indicator of domestic cat personality. *Anthrozoös*, 25(4), 427–440. <https://doi.org/10.2752/175303712X13479798785779>
- Dias, B. G., Banerjee, S. B., Goodman, J. V., & Ressler, K. J. (2013). Towards new approaches to disorders of fear and anxiety. *Current Opinion in Neurobiology*, 23(3), 346–352. <https://doi.org/10.1016/j.conb.2013.01.013>
- Dinwoodie, I. R., Dwyer, B., Zottola, V., Gleason, D., & Dodman, N. H. (2019). Demographics and comorbidity of behavior problems in dogs. *Journal of Veterinary Behavior*, 32, 62–71.  
<https://doi.org/10.1016/j.jveb.2019.04.007>
- Dochtermann, N. A., Schwab, T., Anderson Berdal, M., Dalos, J., & Royauté, R. (2019). The heritability of behavior: a meta-analysis. *Journal of Heredity*, 110(4), 403–410. <https://doi.org/10.1093/jhered/esz023>
- Dochtermann, N. A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic variation to personality variation: heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142201.  
<https://doi.org/10.1098/rspb.2014.2201>
- Dreschel, N. A. (2010). The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science*, 125(3–4), 157–162.  
<https://doi.org/10.1016/j.applanim.2010.04.003>
- Driscoll, C. A., Macdonald, D. W., & O'Brien, S. J. (2009). From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences*, 106, 9971–9978.  
<https://doi.org/10.1073/pnas.0901586106>
- Duffy, D. L., de Moura, R. T. D., & Serpell, J. A. (2017). Development and evaluation of the Fe-BARQ: A new survey instrument for measuring behavior in domestic cats (*Felis s. catus*). *Behavioural Processes*, 141, 329–341. <https://doi.org/10.1016/j.beproc.2017.02.010>
- Ellis, S. L. H., Thompson, H., Guijarro, C., & Zulch, H. E. (2015). The influence of body region, handler familiarity and order of region handled on the

- domestic cat's response to being stroked. *Applied Animal Behaviour Science*, 173, 60–67. <https://doi.org/10.1016/j.applanim.2014.11.002>
- Evans, R., Lyons, M., Brewer, G., & Tucci, S. (2019). The purrfect match: The influence of personality on owner satisfaction with their domestic cat (*Felis silvestris catus*). *Personality and Individual Differences*, 138(July 2018), 252–256. <https://doi.org/10.1016/j.paid.2018.10.011>
- Farnworth, M. J., Chen, R., Packer, R. M. A., Caney, S. M. A., & Gunn-Moore, D. A. (2016). Flat feline faces: Is brachycephaly associated with respiratory abnormalities in the domestic cat (*Felis catus*)? *PLOS ONE*, 11(8), e0161777. <https://doi.org/10.1371/journal.pone.0161777>
- Feaver, J., Mendl, M., & Bateson, P. (1986). A method for rating the individual distinctiveness of domestic cats. *Animal Behaviour*, 34(4), 1016–1025. [https://doi.org/10.1016/S0003-3472\(86\)80160-9](https://doi.org/10.1016/S0003-3472(86)80160-9)
- Feldman, H. N. (1994). Methods of scent marking in the domestic cat. *Canadian Journal of Zoology*, 72(6), 1093–1099. <https://doi.org/10.1139/z94-147>
- Finka, L. R., Ward, J., Farnworth, M. J., & Mills, D. S. (2019). Owner personality and the wellbeing of their cats share parallels with the parent-child relationship. *PLOS ONE*, 14(2), e0211862. <https://doi.org/10.1371/journal.pone.0211862>
- Foster, S., & Ijichi, C. (2017). The association between infrared thermal imagery of core eye temperature, personality, age and housing in cats. *Applied Animal Behaviour Science*, 189, 79–84. <https://doi.org/10.1016/j.applanim.2017.01.004>
- Fox, J. (2003). Effect displays in R for generalised linear models. *Journal of Statistical Software*, 8(15), 1–27. <https://doi.org/10.18637/jss.v008.i15>
- Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (3rd ed.). Sage Publications, Inc. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Foyer, P., Wilsson, E., & Jensen, P. (2016). Levels of maternal care in dogs affect adult offspring temperament. *Scientific Reports*, 6(1), 19253. <https://doi.org/10.1038/srep19253>
- Foyer, P., Wilsson, E., Wright, D., & Jensen, P. (2013). Early experiences modulate stress coping in a population of German shepherd dogs. *Applied Animal Behaviour Science*, 146(1–4), 79–87. <https://doi.org/10.1016/j.applanim.2013.03.013>
- Freeman, H., Gosling, S. D., & Schapiro, S. J. (2011). Comparison of methods for assessing personality in nonhuman primates. In *Personality and Temperament in Nonhuman Primates* (pp. 17–40). Springer New York. [https://doi.org/10.1007/978-1-4614-0176-6\\_2](https://doi.org/10.1007/978-1-4614-0176-6_2)
- Fukimoto, N., Melo, D., Palme, R., Zanella, A. J., & Mendonça-Furtado, O. (2020). Are cats less stressed in homes than in shelters? A study of personality and faecal cortisol metabolites. *Applied Animal Behaviour Science*, 224, 104919. <https://doi.org/10.1016/j.applanim.2019.104919>
- Funder, D. C., & Ozer, D. J. (2019). Evaluating effect size in psychological research: sense and nonsense. *Advances in Methods and Practices in Psychological Science*, 2(2), 156–168. <https://doi.org/10.1177/2515245919847202>
- Galef, B. G., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience*, 55(6), 489–499. [https://doi.org/https://doi.org/10.1641/0006-3568\(2005\)055\[0489:SLIAES\]2.0.CO;2](https://doi.org/https://doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2)

- Gandolfi, B., & Alhaddad, H. (2015). Investigation of inherited diseases in cats. *Journal of Feline Medicine and Surgery*, 17(5), 405–415. <https://doi.org/10.1177/1098612X15581133>
- Gandolfi, B., Alhaddad, H., Abdi, M., Bach, L. H., Creighton, E. K., Davis, B. W., Decker, J. E., Dodman, N. H., Grahn, J. C., Grahn, R. A., Haase, B., Haggstrom, J., Hamilton, M. J., Helps, C. R., Kurushima, J. D., Lohi, H., Longeri, M., Malik, R., Meurs, K. M., ... Lyons, L. A. (2018). Applications and efficiencies of the first cat 63K DNA array. *Scientific Reports*, 8(1), 7024. <https://doi.org/10.1038/s41598-018-25438-0>
- Garner, J. P. (2005). Stereotypies and other abnormal repetitive behaviors: Potential impact on validity, reliability, and replicability of scientific outcomes. *ILAR Journal*, 46(2), 106–117. <https://doi.org/10.1093/ilar.46.2.106>
- Gartland, L. A., Firth, J. A., Laskowski, K. L., Jeanson, R., & Ioannou, C. C. (2022). Sociability as a personality trait in animals: methods, causes and consequences. *Biological Reviews*, 97(2), 802–816. <https://doi.org/10.1111/brv.12823>
- Gartner, M. C. (2015). Pet personality: A review. *Personality and Individual Differences*, 75, 102–113. <https://doi.org/10.1016/j.paid.2014.10.042>
- Gartner, M. C., Powell, D. M., & Weiss, A. (2014). Personality structure in the domestic cat (*Felis silvestris catus*), scottish wildcat (*Felis silvestris grampia*), clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), and african lion (*Panthera leo*): A comparative study. *Journal of Comparative Psychology*, 128(4), 414–426. <https://doi.org/10.1037/a0037104.supp>
- Gartner, M. C., & Weiss, A. (2013). Personality in felids: a review. *Applied Animal Behaviour Science*, 144(1–2), 1–13. <https://doi.org/10.1016/j.applanim.2012.11.010>
- Gignac, G. E., & Szodorai, E. T. (2016). Effect size guidelines for individual differences researchers. *Personality and Individual Differences*, 102, 74–78. <https://doi.org/10.1016/j.paid.2016.06.069>
- Goldberg, L. R. (1990). An alternative “description of personality”: the big-five factor structure. *Journal of Personality and Social Psychology*, 59(6), 1216–1229. <https://doi.org/10.1037//0022-3514.59.6.1216>
- Goldstein-Piekarski, A. N., Williams, L. M., & Humphreys, K. (2016). A trans-diagnostic review of anxiety disorder comorbidity and the impact of multiple exclusion criteria on studying clinical outcomes in anxiety disorders. *Translational Psychiatry*, 6(6), e847–e847. <https://doi.org/10.1038/tp.2016.108>
- Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, 127(1), 45–86. <https://doi.org/10.1037/0033-2909.127.1.45>
- Gosling, S. D. (2008). Personality in non-human animals. *Social and Personality Psychology Compass*, 2(2), 985–1001. <https://doi.org/10.1111/j.1751-9004.2008.00087.x>
- Gosling, S. D., Kwan, V. S. Y., & John, O. P. (2003). A dog’s got personality: A cross-species comparative approach to personality judgments in dogs and humans. *Journal of Personality and Social Psychology*, 85(6), 1161–1169. <https://doi.org/10.1037/0022-3514.85.6.1161>

- Greenwell, B., Boehmke, B., Cunningham, J., & Developers, G. (2020). *gbm: Generalized Boosted Regression Models*. <https://cran.r-project.org/package=gbm>
- Greenwell, B. M., & Boehmke, B. C. (2020). Variable importance plots—An introduction to the vip package. *The R Journal*, *12*(1), 343–366. <https://doi.org/10.32614/RJ-2020-013>
- Grigg, E. K., & Kogan, L. R. (2019). Owners' attitudes, knowledge, and care practices: exploring the implications for domestic cat behavior and welfare in the home. *Animals*, *9*(11), 978. <https://doi.org/10.3390/ani9110978>
- Gunn-Moore, D., Bessant, C., & Malik, R. (2008). Breed-related disorders of cats. *Journal of Small Animal Practice*, *49*, 167–168. <https://doi.org/10.1111/j.1748-5827.2008.00572.x>
- Ha, D., & Ha, J. (2017). A subjective domestic cat (*Felis silvestris catus*) temperament assessment results in six independent dimensions. *Behavioural Processes*, *141*, 351–356. <https://doi.org/10.1016/j.beproc.2017.03.012>
- Hart, B. L., & Hart, L. A. (2013a). Feline behavioural problems and solutions. In D. C. Turner & P. Bateson (Eds.), *The Domestic Cat: The Biology of its Behaviour* (3rd ed., pp. 201–212). Cambridge University Press. <https://doi.org/10.1017/CBO9781139177177.019>
- Hart, B. L., & Hart, L. A. (2013b). *Your Ideal Cat: Insights into Breed and Gender Differences in Cat Behaviour*. Purdue University Press.
- Hastie, T. (2020). *gam: Generalized Additive Models*. <https://cran.r-project.org/package=gam>
- Hattori, M., Saito, A., Nagasawa, M., Kikusui, T., & Yamamoto, S. (2022). Changes in cat facial morphology are related to interaction with humans. *Animals*, *12*(3493), 1–11. <https://doi.org/10.3390/ani12243493>
- Herron, M. E. (2010). Advances in understanding and treatment of feline inappropriate elimination. *Topics in Companion Animal Medicine*, *25*(4), 195–202. <https://doi.org/10.1053/J.TCAM.2010.09.005>
- Horwitz, D. F. (1997). Behavioral and environmental factors associated with elimination behavior problems in cats: a retrospective study. *Applied Animal Behaviour Science*, *52*(1–2), 129–137. [https://doi.org/10.1016/S0168-1591\(96\)01073-8](https://doi.org/10.1016/S0168-1591(96)01073-8)
- Howard, M. C. (2016). A review of exploratory factor analysis decisions and overview of current practices: What we are doing and how can we improve? *International Journal of Human-Computer Interaction*, *32*(1), 51–62. <https://doi.org/10.1080/10447318.2015.1087664>
- Hsu, Y., & Sun, L. (2010). Factors associated with aggressive responses in pet dogs. *Applied Animal Behaviour Science*, *123*(3–4), 108–123. <https://doi.org/10.1016/j.applanim.2010.01.013>
- Hudson, R., Chacha, J., Bánszegi, O., Szenczi, P., & Rödel, H. G. (2017). Highly stable individual differences in the emission of separation calls during early development in the domestic cat. *Developmental Psychobiology*, *59*(3), 367–374. <https://doi.org/10.1002/dev.21501>
- Hudson, R., Rangassamy, M., Saldaña, A., Bánszegi, O., & Rödel, H. G. (2015). Stable individual differences in separation calls during early development in cats and mice. *Frontiers in Zoology*, *12*(12). <https://doi.org/10.1186/1742-9994-12-S1-S12>

- Ines, M., Ricci-Bonot, C., & Mills, D. S. (2021). My cat and me—A study of cat owner perceptions of their bond and relationship. *Animals*, *11*(6), 1601. <https://doi.org/10.3390/ani11061601>
- Jakuba, T., Polcová, Z., Fedáková, D., Kottferová, J., Mareková, J., Fejsáková, M., Ondrašovičová, O., & Ondrašovič, M. (2013). Differences in evaluation of a dog's temperament by individual members of the same household. *Society & Animals*, *21*(6), 582–589. <https://doi.org/10.1163/15685306-12341314>
- Jones, A. C. (2008). *Development and Validation of a Dog Personality Questionnaire* [University of Texas at Austin, Austin, TX, USA]. <http://hdl.handle.net/2152/18124>
- Karn-Buehler, J., & Kuhne, F. (2021). Perception of stress in cats by German cat owners and influencing factors regarding veterinary care. *Journal of Feline Medicine and Surgery*, 1–10. <https://doi.org/10.1177/1098612X211041307>
- Kelly, S. A., Panhuis, T. M., & Stoehr, A. M. (2012). Phenotypic plasticity: molecular mechanisms and adaptive significance. *Comprehensive Physiology*, *2*, 1417–1439. <https://doi.org/10.1002/cphy.c110008>
- King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality*, *31*(2), 257–271. <https://doi.org/10.1006/jrpe.1997.2179>
- Krajcarz, M. T. M., Krajcarz, M. T. M., Baca, M., Golubiński, M., Bielichová, Z., Bulatović, J., Csippán, P., Dimitrijević, V., Kyselý, R., Makowiecki, D., Marciszak, A., Marković, N., Mladenović, M., Van Neer, W., Obada, T., Živaljević, I., Bulatović, A., Ivanišević, V., Pop-Lazić, S., ... Popović, D. (2022). The history of the domestic cat in Central Europe. *Antiquity*, *96*(390), 1628–1633. <https://doi.org/10.15184/aqy.2022.128>
- Kuhn, M. (2021). *caret: Classification and Regression Training*. <https://cran.r-project.org/package=caret>
- Kurushima, J. D., Ikram, S., Knudsen, J., Bleiberg, E., Grahn, R. A., & Lyons, L. A. (2012). Cats of the pharaohs: genetic comparison of Egyptian cat mummies to their feline contemporaries. *Journal of Archaeological Science*, *39*(10), 3217–3223. <https://doi.org/10.1016/j.jas.2012.05.005>
- Lee, C. M., Ryan, J. J., & Kreiner, D. S. (2007). Personality in domestic cats. *Psychological Reports*, *100*, 27–29. <https://doi.org/10.2466/pro.100.1.27-29>
- Leech, L. E., Preziosi, R., Stoycheva, R., & Pastorino, G. Q. (2022). The effects of owner and domestic cat (*Felis catus*) demographics on cat personality traits. *Applied Animal Behaviour Science*, *248*, 105570. <https://doi.org/10.1016/j.applanim.2022.105570>
- Lenth, R. (2021). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. <https://cran.r-project.org/package=emmeans>
- Lesch, R., Kitchener, A. C., Hantke, G., Kotrschal, K., & Fitch, W. T. (2022). Cranial volume and palate length of cats, *Felis* spp., under domestication, hybridization and in wild populations. *Royal Society Open Science*, *9*(210477), 1–9. <https://doi.org/10.1098/rsos.210477>
- Levitis, D. A., Lidicker, W. Z., & Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour*, *78*(1), 103–110. <https://doi.org/10.1016/j.anbehav.2009.03.018>
- Ley, J. M., McGreevy, P., & Bennett, P. C. (2009). Inter-rater and test–retest reliability of the Monash Canine Personality Questionnaire-Revised (MCPQ-R). *Applied Animal Behaviour Science*, *119*(1–2), 85–90. <https://doi.org/10.1016/j.applanim.2009.02.027>

- Lipinski, M. J., Froenicke, L., Baysac, K. C., Billings, N. C., Leutenegger, C. M., Levy, A. M., Longeri, M., Niini, T., Ozpinar, H., Slater, M. R., Pedersen, N. C., & Lyons, L. A. (2008). The ascent of cat breeds: Genetic evaluations of breeds and worldwide random-bred populations. *Genomics*, *91*(1), 12–21. <https://doi.org/10.1016/j.ygeno.2007.10.009>
- Litchfield, C. A., Quinton, G., Tindle, H., Chiera, B., Kikillus, K. H., & Roetman, P. (2017). The ‘Feline Five’: an exploration of personality in pet cats (*Felis catus*). *PLoS ONE*, *12*(8), 1–17. <https://doi.org/10.1371/journal.pone.0183455>
- Litwin, M. (2003). *How to Assess and Interpret Survey Psychometrics* (2nd ed.). SAGE Publications, Inc. <https://doi.org/10.4135/9781412984409>
- Lowe, S. E., & Bradshaw, J. W. S. (2001). Ontogeny of individuality in the domestic cat in the home environment. *Animal Behaviour*, *61*, 231–237. <https://doi.org/10.1006/anbe.2000.1545>
- Lowe, S. E., & Bradshaw, J. W. S. (2002). Responses of pet cats to being held by an unfamiliar person, from weaning to three years of age. *Anthrozoos*, *15*(1), 69–79. <https://doi.org/10.2752/089279302786992702>
- Luescher, A. U. (2003). Diagnosis and management of compulsive disorders in dogs and cats. *Veterinary Clinics of North America: Small Animal Practice*, *33*(2), 253–267. [https://doi.org/10.1016/S0195-5616\(02\)00100-6](https://doi.org/10.1016/S0195-5616(02)00100-6)
- Machado, D. de S., Gonçalves, L. da S., Vicentini, R. R., Ceballos, M. C., & Sant’anna, A. C. (2020). Beloved whiskers: management type, care practices and connections to welfare in domestic cats. *Animals* *2020*, Vol. 10, Page 2308, *10*(12), 2308. <https://doi.org/10.3390/ANI10122308>
- Mangiafico, S. (2019, May 18). *rcompanion: Functions to Support Extension Education Program Evaluation*. <https://cran.r-project.org/package=rcompanion>
- Martell-Moran, N. K., Solano, M., & Townsend, H. G. G. (2018). Pain and adverse behavior in declawed cats. *Journal of Feline Medicine and Surgery*, *20*(4), 280–288. <https://doi.org/10.1177/1098612X17705044>
- Martos Martinez-Caja, A., Rosseau, J., Vervaecke, H., & Moons, C. P. H. (2021). Behavior and health issues in Bengal cats as perceived by their owners: a descriptive study. *Journal of Veterinary Behavior*, *41*, 12–21. <https://doi.org/10.1016/j.jveb.2020.10.007>
- Maskey, R., Fei, J., & Nguyen, H.-O. (2018). Use of exploratory factor analysis in maritime research. *The Asian Journal of Shipping and Logistics*, *34*(2), 91–111. <https://doi.org/10.1016/j.ajsl.2018.06.006>
- McCune, S. (1995). The impact of paternity and early socialisation on the development of cats’ behaviour to people and novel objects. *Applied Animal Behaviour Science*, *45*(1–2), 109–124. [https://doi.org/10.1016/0168-1591\(95\)00603-P](https://doi.org/10.1016/0168-1591(95)00603-P)
- McDowell, L. J., Wells, D. L., Hepper, P. G., & Dempster, M. (2016). Lateral bias and temperament in the domestic cat (*Felis silvestris*). *Journal of Comparative Psychology*, *130*(4), 313–320. <https://doi.org/10.1037/com0000030>
- McLean, M. A., Cobham, V. E., Simcock, G., Kildea, S., & King, S. (2019). Toddler temperament mediates the effect of prenatal maternal stress on childhood anxiety symptomatology: The QF2011 Queensland flood study. *International Journal of Environmental Research and Public Health*, *16*(1998), 1–23. <https://doi.org/10.3390/ijerph16111998>

- Menchetti, L., Calipari, S., Guelfi, G., Catanzaro, A., & Diverio, S. (2018). My dog is not my cat: Owner perception of the personalities of dogs and cats living in the same household. *Animals*, *8*(6), 80. <https://doi.org/10.3390/ani8060080>
- Menor-Campos, D. J., Ruiz-Soriano, C., & Serpell, J. (2021). Spanish validation of the Fe-BARQ questionnaire: a replication study. *Journal of Veterinary Behavior*, *46*, 101–114. <https://doi.org/10.1016/j.jveb.2021.09.002>
- Menotti-Raymond, M., David, V. A., Pflueger, S. M., Lindblad-Toh, K., Wade, C. M., O'Brien, S. J., & Johnson, W. E. (2008). Patterns of molecular genetic variation among cat breeds. *Genomics*, *91*(1), 1–11. <https://doi.org/10.1016/j.ygeno.2007.08.008>
- Mikkola, S., Salonen, M., Hakanen, E., & Lohi, H. (2022). Fearfulness associates with problematic behaviors and poor socialization in cats. *iScience*, *25*(10), 105265. <https://doi.org/10.1016/j.isci.2022.105265>
- Mikkola, S., Salonen, M., Hakanen, E., & Lohi, H. (2023). Feline litter box issues associate with cat personality, breed, and age at sterilization. *Journal of the American Veterinary Medical Association*, 1–9. <https://doi.org/10.2460/javma.22.10.0441>
- Mikkola, S., Salonen, M., Hakanen, E., Sulkama, S., & Lohi, H. (2021). Reliability and validity of seven feline behavior and personality traits. *Animals*, *11*(1991). <https://doi.org/10.3390/ani11071991>
- Mikkola, S., Salonen, M., Puurunen, J., Hakanen, E., Sulkama, S., Araujo, C., & Lohi, H. (2021). Aggressive behaviour is affected by demographic, environmental and behavioural factors in purebred dogs. *Scientific Reports* *2021 11:1*, *11*(1), 1–10. <https://doi.org/10.1038/s41598-021-88793-5>
- Mills, D. S., Demontigny-Bédard, I., Gruen, M., Klinck, M. P., McPeake, K. J., Barcelos, A. M., Hewison, L., Van Haevermaet, H., Denenberg, S., Hauser, H., Koch, C., Ballantyne, K., Wilson, C., Mathkari, C. V., Pounder, J., Garcia, E., Darder, P., Fatjó, J., & Levine, E. (2020). Pain and problem behavior in cats and dogs. *Animals*, *10*(2), 318. <https://doi.org/10.3390/ani10020318>
- Montague, M. J., Li, G., Gandolfi, B., Khan, R., Aken, B. L., Searle, S. M. J., Minx, P., Hillier, L. W., Koboldt, D. C., Davis, B. W., Driscoll, C. A., Barr, C. S., Blackistone, K., Quilez, J., Lorente-Galdos, B., Marques-Bonet, T., Alkan, C., Thomas, G. W. C., Hahn, M. W., ... Warren, W. C. (2014). Comparative analysis of the domestic cat genome reveals genetic signatures underlying feline biology and domestication. *Proceedings of the National Academy of Sciences*, *111*(48), 17230–17235. <https://doi.org/10.1073/pnas.1410083111>
- Monteiro, B. P., Lee, N. H., & Steagall, P. V. (2023). Can cat caregivers reliably assess acute pain in cats using the Feline Grimace Scale? A large bilingual global survey. *Journal of Feline Medicine and Surgery*, *25*(1), 1–9. <https://doi.org/10.1177/1098612X221145499>
- Morais, L. H., Schreiber IV, H. L., & Mazmanian, S. K. (2021). The gut microbiota – brain axis in behaviour and brain disorders. *Nature Reviews Microbiology*, *19*, 241–255. <https://doi.org/10.1038/s41579-020-00460-0>
- Naderi, M. M., Rafiei, S. M., Sattari, B., Ale-Davoudl, S. J., Seif, A. A., & Bokaei, S. (2011). The first study on classification of Iranian domestic cats' behavior problems and their associated risk factors. *Global Veterinaria*, *6*(3), 339–345. [http://www.idosi.org/gv/gv6\(3\)11/24.pdf](http://www.idosi.org/gv/gv6(3)11/24.pdf)
- National Research Council (NRC). (2006). *Nutrient Requirements for Dogs and Cats*. National Academy Press.

- Natoli, E., Litchfield, C., & Pontier, D. (2022). Coexistence between humans and ‘misunderstood’ domestic cats in the Anthropocene: Exploring behavioural plasticity as a gatekeeper of evolution. *Animals*, 12(13), 1717. <https://doi.org/10.3390/ani12131717>
- Neilson, J. (2004). Thinking outside the box: feline elimination. *Journal of Feline Medicine and Surgery*, 6(1), 5–11. <https://doi.org/10.1016/j.jfms.2003.09.008>
- Nilson, S. M., Gandolfi, B., Grahn, R. A., Kurushima, J. D., Lipinski, M. J., Randi, E., Waly, N. E., Driscoll, C., Murua Escobar, H., Schuster, R. K., Maruyama, S., Labarthe, N., Chomel, B. B., Ghosh, S. K., Ozpinar, H., Rah, H.-C., Millán, J., Mendes-de-Almeida, F., Levy, J. K., ... Lyons, L. A. (2022). Genetics of randomly bred cats support the cradle of cat domestication being in the Near East. *Heredity*, 129(6), 346–355. <https://doi.org/10.1038/s41437-022-00568-4>
- Niskanen, J., Salonen, M. K., & Puurunen, J. (2021). *airGLMs*. *GitHub repository*. <https://github.com/JNisk/airGLMs>
- Normando, S., Venturini, T., Filugelli, L., Bonetti, O., Mutinelli, F., & Contalbrigo, L. (2022). Cat-human bond: Satisfaction and behavioural complaints among Italian respondents. *Applied Animal Behaviour Science*, 256, 105749. <https://doi.org/10.1016/j.applanim.2022.105749>
- Otoni, C., & Neer, W. Van. (2020). The dispersal of the domestic cat. *Near Eastern Archaeology*, 83(1), 38–45. <https://doi.org/10.1086/707312>
- Otoni, C., Van Neer, W., De Cupere, B., Daligault, J., Guimaraes, S., Peters, J., Spassov, N., Prendergast, M. E., Boivin, N., Morales-Muñiz, A., Bălăşescu, A., Becker, C., Benecke, N., Boroneant, A., Buitenhuis, H., Chahoud, J., Crowther, A., Llorente, L., Manaseryan, N., ... Geigl, E.-M. (2017). The palaeogenetics of cat dispersal in the ancient world. *Nature Ecology & Evolution*, 1(0139), 1–7. <https://doi.org/10.1038/s41559-017-0139>
- Overall, K. L., & Dunham, A. E. (2002). Clinical features and outcome in dogs and cats with obsessive-compulsive disorder: 126 cases (1989–2000). *Journal of the American Veterinary Medical Association*, 221(10), 1445–1452. <https://doi.org/10.2460/javma.2002.221.1445>
- Overall, K. L., Tiira, K., Broach, D., & Bryant, D. (2014). Genetics and behavior: A guide for practitioners. *Veterinary Clinics of North America: Small Animal Practice*, 44(3), 483–505. <https://doi.org/10.1016/j.cvsm.2014.01.006>
- Petsofi Ltd. Retrieved June 3, 2021, from <https://petsofi.com/>
- Pontier, D., Rioux, N., & Heizmann, A. (1995). Evidence of selection on the orange allele in the domestic cat *Felis catus*: the role of social structure. *Oikos*, 73(3), 299–308. <https://doi.org/10.2307/3545954>
- Porters, N., de Rooster, H., Verschuere, K., Polis, I., & Moons, C. P. H. (2014). Development of behavior in adopted shelter kittens after gonadectomy performed at an early age or at a traditional age. *Journal of Veterinary Behavior*, 9(5), 196–206. <https://doi.org/10.1016/j.jveb.2014.05.003>
- Posluns, J. A., Anderson, R. E., & Walsh, C. J. (2017). Comparing two canine personality assessments: Convergence of the MCPQ-R and DPQ and consensus between dog owners and dog walkers. *Applied Animal Behaviour Science*, 188, 68–76. <https://doi.org/10.1016/j.applanim.2016.12.013>
- Preacher, K. J., & MacCallum, R. C. (2003). Repairing Tom Swift’s electric factor analysis machine. *Understanding Statistics*, 2(1), 13–43. [https://doi.org/10.1207/S15328031US0201\\_02](https://doi.org/10.1207/S15328031US0201_02)

- Pryor, P. A., Hart, B. L., Bain, M. J., & Cliff, K. D. (2001). Causes of urine marking in cats and effects of environmental management on frequency of marking. *Journal of the American Veterinary Medical Association*, 219(12), 1709–1713. <https://doi.org/10.2460/javma.2001.219.1709>
- Puurunen, J., Hakanen, E., Salonen, M. K., Mikkola, S., Sulkama, S., Araujo, C., & Lohi, H. (2020). Inadequate socialisation, inactivity, and urban living environment are associated with social fearfulness in pet dogs. *Scientific Reports*, 10(1), 3527. <https://doi.org/10.1038/s41598-020-60546-w>
- R Core Team. (2021). *R: A language and environment for statistical computing* (4.1.1). R Foundation for Statistical Computing. <https://www.r-project.org/>
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Reisner, I. R., Houpt, K. A., Erb, H. N., & Quimby, F. W. (1994). Friendliness to humans and defensive aggression in cats: The influence of handling and paternity. *Physiology & Behavior*, 55(6), 1119–1124. [https://doi.org/10.1016/0031-9384\(94\)90396-4](https://doi.org/10.1016/0031-9384(94)90396-4)
- Revelle, W. (2021). *psych: Procedures for Psychological, Psychometric, and Personality Research*. <https://cran.r-project.org/package=psych>
- Richards, E. J. (2006). Inherited epigenetic variation – revisiting soft inheritance. *Nature Reviews Genetics*, 7, 395–401.
- Robinson, D., Hayes, A., & Couch, S. (2021). *broom: Convert Statistical Analysis Objects into Tidy Tibbles*. <https://cran.r-project.org/package=broom>
- Rochlitz, I. (2005). A review of the housing requirements of domestic cats (*Felis silvestris catus*) kept in the home. *Applied Animal Behaviour Science*, 93(1–2), 97–109. <https://doi.org/10.1016/j.applanim.2005.01.002>
- Rodan, I. (2010). Understanding feline behavior and application for appropriate handling and management. *Topics in Companion Animal Medicine*, 25(4), 178–188. <https://doi.org/10.1053/j.tcam.2010.09.001>
- Salman, M. D., Hutchison, J., Ruch-Gallie, R., Kogan, L., New, J. C., Kass, P. H., & Scarlett, J. M. (2010). *Behavioral reasons for relinquishment of dogs and cats to 12 shelters*. [https://doi.org/10.1207/S15327604JAWS0302\\_2](https://doi.org/10.1207/S15327604JAWS0302_2)
- Salonen, M. (2020). *Complex traits, complex results: The genetic, demographic, and environmental factors of cat and dog behaviour* [Unigrafia]. <http://hdl.handle.net/10138/320181>
- Salonen, M., Mikkola, S., Hakanen, E., Sulkama, S., Puurunen, J., & Lohi, H. (2021). Reliability and validity of a dog personality and unwanted behavior survey. *Animals*, 11(5), 1234. <https://doi.org/10.3390/ani11051234>
- Salonen, M., Mikkola, S., Niskanen, J. E., Hakanen, E., Sulkama, S., Puurunen, J., & Lohi, H. (2023). Breed, age, and social environment are associated with personality traits in dogs. *iScience*, 26(5), 106691. <https://doi.org/10.1016/j.isci.2023.106691>
- Salonen, M., Sulkama, S., Mikkola, S., Puurunen, J., Hakanen, E., Tiira, K., Araujo, C., & Lohi, H. (2020). Prevalence, comorbidity, and breed differences in canine anxiety in 13,700 Finnish pet dogs. *Scientific Reports*, 10(1), 2962. <https://doi.org/10.1038/s41598-020-59837-z>
- Salonen, M., Vapalahti, K., Tiira, K., Mäki-Tanila, A., & Lohi, H. (2019). Breed differences of heritable behaviour traits in cats. *Scientific Reports*, 9(1), 7949. <https://doi.org/10.1038/s41598-019-44324-x>

- Sawyer, L. S., Moon-Fanelli, A. A., & Dodman, N. H. (1999). Psychogenic alopecia in cats: 11 cases (1993-1996). *Journal of the American Veterinary Medical Association*, 214(1), 71–74.
- Schwartz, S. (2002). Separation anxiety syndrome in cats: 136 cases (1991-2000). *Journal of the American Veterinary Medical Association*, 220(7), 1028–1033. <https://doi.org/10.2460/javma.2002.220.1028>
- Serpell, J. A. (1996). Evidence for an association between pet behavior and owner attachment levels. *Applied Animal Behaviour Science*, 47(1–2), 49–60. [https://doi.org/10.1016/0168-1591\(95\)01010-6](https://doi.org/10.1016/0168-1591(95)01010-6)
- Sheriff, M. J., Dantzer, B., Delehanty, B., Palme, R., & Boonstra, R. (2011). Measuring stress in wildlife: techniques for quantifying glucocorticoids. *Oecologia*, 166(4), 869–887. <https://doi.org/10.1007/s00442-011-1943-y>
- Shin, Y.-J., & Shin, N.-S. (2017). Relationship between sociability toward humans and physiological stress in dogs. *Journal of Veterinary Medical Science*, 79(7), 1278–1283. <https://doi.org/10.1292/jvms.16-0403>
- Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin*, 86(2), 420–428. <https://doi.org/10.1037/0033-2909.86.2.420>
- Siegford, J. M., Walshaw, S. O., Brunner, P., & Zanella, A. J. (2003). Validation of a temperament test for domestic cats. *Anthrozoös*, 16(4), 332–351. <https://doi.org/10.2752/089279303786991982>
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *The Quarterly Review of Biology*, 79(3), 241–277. <https://doi.org/10.1086/422893>
- Spain, C. V., Scarlett, J. M., & Houpt, K. A. (2004). Long-term risks and benefits of early-age gonadectomy in cats. *Journal of the American Veterinary Medical Association*, 224(3), 372–379. <https://doi.org/10.2460/JAVMA.2004.224.372>
- Ståhl, A., Salonen, M., Hakanen, E., Mikkola, S., Sulkama, S., Lahti, J., & Lohi, H. (2023). Pet and owner personality and mental wellbeing associate with attachment to cats and dogs. *iScience*, 108423. <https://doi.org/10.1016/j.isci.2023.108423>
- Stanton, L. A., Sullivan, M. S., & Fazio, J. M. (2015). A standardized ethogram for the felidae: a tool for behavioral researchers. *Applied Animal Behaviour Science*, 173, 3–16. <https://doi.org/10.1016/j.applanim.2015.04.001>
- Stella, J., Croney, C., & Buffington, T. (2013). Effects of stressors on the behavior and physiology of domestic cats. *Applied Animal Behaviour Science*, 143(2–4), 157–163. <https://doi.org/10.1016/j.applanim.2012.10.014>
- Stella, J. L., & Buffington, C. A. T. (2016). Environmental strategies to promote health and wellness. In S. Little (Ed.), *August's Consultations in Feline Internal Medicine, Volume 7* (pp. 718–736). Elsevier. <https://doi.org/10.1016/B978-0-323-22652-3.00073-6>
- Stella, J. L., & Croney, C. C. (2016). Environmental aspects of domestic cat care and management: implications for cat welfare. *The Scientific World Journal*, 6296315, 1–7. <https://doi.org/10.1155/2016/6296315>
- Stelow, E. A., Bain, M. J., & Kass, P. H. (2016). The relationship between coat color and aggressive behaviors in the domestic cat. *Journal of Applied Animal Welfare Science*, 19(1), 1–15. <https://doi.org/10.1080/10888705.2015.1081820>

- Strickler, B. L., & Shull, E. A. (2013). An owner survey of toys, activities, and behavior problems in indoor cats. *Journal of Veterinary Behavior: Clinical Applications and Research*, 9(5), 207–214. <https://doi.org/10.1016/j.jveb.2014.06.005>
- Tabachnick, B. G., & Fidell, L. S. (2014). *Using Multivariate Statistics: Pearson New International Edition* (6th ed.). Pearson Education Limited.
- Takeuchi, Y., & Mori, Y. (2009). Behavioral profiles of feline breeds in Japan. *Journal of Veterinary Medical Science*, 71(8), 1053–1057. <https://doi.org/10.1292/jvms.71.1053>
- Tamimi, N., Malmasi, A., Talebi, A., Tamimi, F., & Amini, A. (2015). A survey of feline behavioral problems in Tehran. *Veterinary Research Forum*, 6(2), 143–147. <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4522528&tool=pmcentrez&rendertype=abstract>
- The American Society for the Prevention of Cruelty to Animals. (2013). *MYM Meet Your Match® Feline-ality™ manual and training guide*. [https://www.aspcapro.org/sites/default/files/Feline-ality Guide\\_PRO.pdf](https://www.aspcapro.org/sites/default/files/Feline-ality%20Guide_PRO.pdf)
- The International Cat Association. (2018). Cat breeds. Retrieved November 27, 2023, from <https://tica.org/breeds/browse-all-breeds>
- Tiira, K., & Lohi, H. (2015). Early life experiences and exercise associate with canine anxieties. *PLoS ONE*, 10(11), 1–16. <https://doi.org/10.1371/journal.pone.0141907>
- Tilley, L. P., & Smith, F. W. J. (Eds.). (2016). *Blackwell's five-minute veterinary consult : Canine and feline* (6th ed.). John Wiley & Sons, Incorporated. <https://ebookcentral-proquest-com.libproxy.helsinki.fi/lib/helsinki-ebooks/detail.action?docID=4435989#>
- Travnik, I. de C., Machado, D. de S., Gonçalves, L. da S., Ceballos, M. C., & Sant'Anna, A. C. (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. <https://doi.org/10.3390/ani10091516>
- Turcsán, B., Wallis, L., Virányi, Z., Range, F., Müller, C. A., Huber, L., & Riemer, S. (2018). Personality traits in companion dogs—Results from the VIDOPET. *PLOS ONE*, 13(4), e0195448. <https://doi.org/10.1371/journal.pone.0195448>
- Turner, D. C. (2021). The mechanics of social interactions between cats and their owners. *Frontiers in Veterinary Science*, 8(650143), 1–6. <https://doi.org/10.3389/fvets.2021.650143>
- Turner, D. C., Feaver, J., Mendl, M., & Bateson, P. (1986). Variation in domestic cat behaviour towards humans: a paternal effect. *Animal Behaviour*, 34(6), 1890–1892. [https://doi.org/10.1016/S0003-3472\(86\)80275-5](https://doi.org/10.1016/S0003-3472(86)80275-5)
- Tynes, V. V., & Sinn, L. (2014). Abnormal repetitive behaviors in dogs and cats. *Veterinary Clinics of North America: Small Animal Practice*, 44(3), 543–564. <https://doi.org/10.1016/j.cvsm.2014.01.011>
- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*, 85(2), 327–345. <https://doi.org/10.1111/j.1469-185X.2009.00104.x>
- van Oers, K., & Sinn, D. L. (2013). Quantitative and molecular genetics of animal personality. In C. Carere & D. Maestripieri (Eds.), *Genetics, ecology, and*

- evolution of animal personalities* (pp. 149–275). University of Chicago Press.
- Vapalahti, K., Virtala, A.-M., Joensuu, T. A., Tiira, K., Tähtinen, J., & Lohi, H. (2016). Health and behavioral survey of over 8000 Finnish cats. *Frontiers in Veterinary Science*, 3. <https://doi.org/10.3389/fvets.2016.00070>
- Vitale, K. R. (2022). The social lives of free-ranging cats. *Animals*, 12(1), 126. <https://doi.org/10.3390/ani12010126>
- Vitale, K. R., Behnke, A. C., & Udell, M. A. R. (2019). Attachment bonds between domestic cats and humans. *Current Biology*, 29(18), R864–R865. <https://doi.org/10.1016/j.cub.2019.08.036>
- Vitale, K. R., & Udell, M. A. R. (2019). The quality of being sociable: The influence of human attentional state, population, and human familiarity on domestic cat sociability. *Behavioural Processes*, 158(October 2018), 11–17. <https://doi.org/10.1016/j.beproc.2018.10.026>
- Vogt, A. H., Rodan, I., Brown, M., Brown, S., Buffington, C. A. T., Forman, M. J. L., Neilson, J., & Sparkes, A. (2010). AAFP-AAHA Feline life stage guidelines. *Journal of Feline Medicine and Surgery*, 12(1), 43–54. <https://doi.org/10.1016/j.jfms.2009.12.006>
- Wan, M., Kubinyi, E., Miklósi, Á., & Champagne, F. (2009). A cross-cultural comparison of reports by German Shepherd owners in Hungary and the United States of America. *Applied Animal Behaviour Science*, 121, 206–213. <https://doi.org/10.1016/j.applanim.2009.09.015>
- Wassink-van der Schot, A. A., Day, C., Morton, J. M., Rand, J., & Phillips, C. J. C. (2016). Risk factors for behavior problems in cats presented to an Australian companion animal behavior clinic. *Journal of Veterinary Behavior: Clinical Applications and Research*, 14, 34–40. <https://doi.org/10.1016/j.jveb.2016.06.010>
- Weinshenker, N. J., & Siegel, A. (2002). Bimodal classification of aggression: affective defense and predatory attack. *Aggression and Violent Behavior*, 7(3), 237–250. [https://doi.org/10.1016/S1359-1789\(01\)00042-8](https://doi.org/10.1016/S1359-1789(01)00042-8)
- Weinstock, M. (2008). *Neuroscience and Biobehavioral Reviews The long-term behavioural consequences of prenatal stress*. 32, 1073–1086. <https://doi.org/10.1016/j.neubiorev.2008.03.002>
- Weiss, E., Gramann, S., Drain, N., Dolan, E., & Slater, M. (2015). Modification of the feline-ality™ assessment and the ability to predict adopted cats' behaviors in their new homes. *Animals*, 5(1), 71–88. <https://doi.org/10.3390/ani5010071>
- Weldon, C. W., Prenter, J., & Taylor, P. W. (2010). Activity patterns of Queensland fruit flies (*Bactrocera tryoni*) are affected by both mass-rearing and sterilization. *Physiological Entomology*, 35(2), 148–153. <https://doi.org/10.1111/j.1365-3032.2010.00726.x>
- Whiten, A. (2019). Cultural evolution in animals. *Annual Review of Ecology, Evolution, and Systematics*, 50(1), 27–48. <https://doi.org/10.1146/annurev-ecolsys-110218-025040>
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. <https://ggplot2.tidyverse.org>
- Wickham, H., François, R., Lionel, H., & Müller, K. (2021). *dplyr: A Grammar of Data Manipulation*. <https://cran.r-project.org/package=dplyr>
- Wilhelmy, J., Serpell, J., Brown, D., & Siracusa, C. (2016). Behavioral associations with breed, coat type, and eye color in single-breed cats. *Journal of*

- Veterinary Behavior*, 13, 80–87.  
<https://doi.org/10.1016/j.jveb.2016.03.009>
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452–461.  
<https://doi.org/10.1016/j.tree.2012.05.001>
- Yamada, R., Kuze-Arata, S., Kiyokawa, Y., & Takeuchi, Y. (2020). Prevalence of 17 feline behavioral problems and relevant factors of each behavior in Japan. *Journal of Veterinary Medical Science*, 82(3), 272–278.  
<https://doi.org/10.1292/jvms.19-0519>
- Zeigler-Hill, V., & Highfill, L. (2010). Applying the interpersonal circumplex to the behavioral styles of dogs and cats. *Applied Animal Behaviour Science*, 124(3–4), 104–112. <https://doi.org/10.1016/j.applanim.2010.02.012>
- Zeileis, A., & Hothorn, T. (2002). Diagnostic Checking in Regression Relationships. *R News*, 2(3), 7–10. <https://cran.r-project.org/doc/Rnews/>
- Ziv, G. (2017). The effects of using aversive training methods in dogs—A review. *Journal of Veterinary Behavior*, 19, 50–60.  
<https://doi.org/10.1016/j.jveb.2017.02.004>