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Feline Research

Behavioral associations with breed, coat type, and eye color in single-breed cats

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ABSTRACT

In this study, behavioral characteristics in purebred cats were hypothesized to associate with breed, eye color, coat color, and coat pattern. Owners of 574 single-breed, registered cats completed the Feline Behavioral Assessment and Research Questionnaire, which generates a standardized behavioral profile incorporating 20 factors. Subjects were also screened for evidence of fear-related aggression, territorial aggression and inappropriate social skills, fear of noises, redirected aggression, separation anxiety, and inappropriate elimination. Subject breeds included Abyssinians, Bengals, Birmans, Burmese, Devon rexes, Maine coons, Norwegian Forest cats, Orientals, Persians, Ragdolls, Siamese, and Tonkinese. Coat colors included agouti, black, brown, cinnamon, blue, lilac, fawn, caramel, taupe, red, cream, blue cream, apricot, and white. Phenotypic variants associated with albinism, tabby and tortoiseshell patterning, inhibition of melanin, production of pheomelanin, and white spotting were represented. Statistical analysis revealed significant differences in the Feline Behavioral Assessment and Research Questionnaire scores and frequency of behavior problems in cats of multiple coat colors, coat patterns, and breeds ($P < 0.05$). Interestingly, nearly all associations between behavior and coat type could be attributed to breed-based behavior differences. Associations independent of breed included increased cat aggression in agouti cats and prey interest in red cats, decreased stranger-directed aggression in piebald cats, and increased likelihood of separation anxiety in Siamese and Tonkinese patterned cats.

Introduction

Precedent exists in multiple species for seeking an association between breed and behavior, as well as between appearance and behavior. Breed differences in aggression and trainability have been documented in dogs via use of a standardized behavioral questionnaire (C-BARQ) (Serpell & Hsu, 2005; Duffy et al., 2008; McGreevy et al., 2013; Ghirlanda et al., 2013). Other studies have found breed-related differences in canine emotionality and aggressiveness, the tendency to approach and withdraw in novel situations, activity and playfulness, predatory behavior, social behavior toward humans, and agonistic signaling (Svartberg, 2006). A 25-item rating method in horses, the Horse Personality Questionnaire, has revealed significant differences among breeds, particularly with regard to anxiousness and excitability (Lloyd et al., 2008).

Veterinarians and cat show judges were reported to perceive differences in behavior among feline breeds. Judges characterized Siamese as demanding of attention and outgoing with strangers, while describing Russian Blues as shy and withdrawn. Veterinarians perceived Siamese to be active and vocal, Persians to be less active and destructive, and Oriental Shorthairs to be more excitable and destructive (Mendl & Harcourt, 2000). When assayed on their perceptions of 15 common breeds, feline veterinary practitioners characterized Bengals as most active, most likely to aggress toward human family members, and most likely to urine mark; Persians were felt to be least active and least likely to use the litter box (Hart et al., 2013). Direct observation of owner-cat interactions revealed more vocalization and initiation of contact by Siamese than Persian cats (Mendl & Harcourt, 2000). A faster decline in exploration and locomotion scores occurred during an open field trial in Siamese, Orientals, and Abyssinians, as compared with Norwegian Forest cats (Marchei et al., 2009).

Selection for a particular color phenotype has also been shown to result in significant changes in behavior. In general, selection for

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a given trait may unintentionally result in selection for a genetically linked phenotype; pleiotropy may also occur, as can sensory deficits that alter behavior (Bergsma & Brown, 1971; Mendl & Harcourt, 2000). Gray-coated rats carrying the dominant agouti allele demonstrated significantly increased wildness and "savagery" relative to rats homozygous for the black (nonagouti) allele; gray and black animals differed in their sense of smell (Keeler, 1942). Nonagouti deer mice were also found to be less active, aggressive, and resistant to handling, and the agouti locus has been suggested as an important modulator of neural melanocortins (Hayssen 1997).

Fawn-colored Korean Jindo dogs exhibited significantly less fearful and submissive reactivity, and significantly more scent-marking behavior, than white-colored Jindos (Kim et al., 2010). Using the Campbell Test, aggression was found to be decreasingly likely in golden, black, and particolored Cocker spaniels (Amat et al., 2009). The likelihood of success in guide dog training was significantly different between black and yellow Labrador retrievers (Batt et al., 2008). Although not more reactive in a novel and potentially frightening situation, Icelandic horses with silver-colored coats and expressing the Arg618Cys mutation in the PMEL/SILV gene were significantly more cautious (Brunberg et al., 2013). Silver foxes artificially selected for reduced aggressiveness and fearfulness during human interaction displayed a corresponding increase in yellow-brown mottling and piebaldness (Trut et al., 2004).

Preliminary evidence for associations between coat color and behavior is also found in cats. When 84 British shorthair kittens were handled by an unfamiliar person, the red, cream, and tortoiseshell subjects showed a longer latency to quieting and increased escape attempts compared to kittens with other coat colors (Mendl & Harcourt, 2000). When seven coat color loci were studied in French domestic cats, cats in progressively more rural environs were found to have correspondingly greater frequencies of the dominant red allele. Because rural populations of the domestic cat are characterized by low densities and a polygynous mating system, researchers postulated that reproductive tactics may differ between red and non-red males, leading to the rural-urban allelic cline (Pontier et al., 1995).

We hypothesized that associations would be found between behavior and breed in purebred cats. In addition, we hypothesized that associations independent of breed would be found between behavior and coat color, coat pattern, and eye color.

Materials and methods

Selection of breeds and phenotypes

Included breeds comprised those recognized by 3 major international cat registries: The International Cat Association, the World Cat Federation, and The Cat Fanciers' Association. Physical characteristics included coat color, coat pattern, and eye color. Each characteristic was subdivided into phenotypes with a known genetic basis. Coat colors reflected allelic variation at the agouti, black/brown (Lyons et al., 2005a; Schmidt-Kuntzel et al., 2005), red (Schmidt-Küntzel et al., 2009), white (Bergsma & Brown, 1971), dilution (Ishida et al., 2006), and dilution modifier loci (Robinson, 1991; Robinson, 1991). These loci are responsible for the agouti, black, brown, cinnamon, blue, lilac, fawn, caramel, taupe, red, cream, blue cream, apricot, and white colors recognized in domestic cats. In addition, coat patterns were selected to represent variation at the following loci: albinism (Thompson et al., 1943; O'Brien et al., 1986; Lyons et al., 2005b; Schmidt-Kuntzel et al. 2005; Imes et al., 2006), tabby patterning (Lomax & Robinson, 1988; Eizirik et al., 2010; Kaelin & Barsh, 2010; Kaelin et al., 2012), inhibition of melanin (Eizirik et al., 2003), production of pheomelanin (Peterschmitt et al., 2009), tortoiseshell patterning (Centerwall & Benirschke 1973), and piebaldness or white spotting (Cooper et al., 2006). See the Supplementary Materials (Item A) for a full list of included patterns, and Figure 1 for representative images. Eye color phenotypes included the copper, orange, amber, yellow, gold, hazel, and green common to most patterns and coat colors (Robinson, 1991). The eye color category also distinguished the blue and odd eyes of cats with a dominant W allele at the white locus (Bergsma & Brown, 1971), as well as blue, chartreuse, aquamarine, albino pink (Robinson, 1991), and albino blue eyes resulting from variation at the albinism locus (Turner et al., 1981).

Characterization of behavioral phenotypes

Behavioral phenotypes for each subject cat were generated via use of a retrospective survey. The basis for this survey constituted the Feline Behavioral Assessment and Research Questionnaire (Fe-BARQ), which uses 100 questionnaire items to generate a standardized behavioral profile composed of 20 discreet factors (Serpell, 2013). See the Supplementary Materials (Item B) for a complete list of factors. These factors, or behavior traits, were previously extracted by factor analysis from cat owners' responses to 149 questions intended to identify the behavior of the subject in multiple common scenarios. Scores represented the frequency of a behavior's occurrence, with increasing scores representing increasing frequency of the behavior addressed by a given question (0 = never, 1 = seldom, 2 = sometimes, 3 = usually, 4 = always). To generate a factor score, the scores for each question contributing to that factor were summed and divided by the number of contributing questions. An "unknown" response was also available for each question; such responses did not contribute to the factor score, and the sum of the contributing scores was divided by 1 less.

In addition to the 20 Fe-BARQ factor scores, the survey was modified to screen for the presence of common behavior pathologies (see Supplementary Materials Item D for the modified Fe-BARQ). None of the original Fe-BARQ questions were altered, but questions consistent with 6 behavior pathologies were identified, and several additional questions were incorporated. Question selection was based on the clinical signs reported for each of the following pathologies: fear-related aggression (Beaver, 2004; Moesta & Crowell-Davis, 2011), territorial aggression or inappropriate play behavior (Landsberg et al., 2003b; Crowell-Davis et al., 2004; Houpt, 2011; Houpt, 2011), redirected aggression (Heath, 2012), fear of noises (Levine, 2012), separation anxiety (Schwartz, 2002; Horowitz, 2012), and inappropriate elimination (both marking and toileting) (Landsberg et al., 2003a; Herron, 2010). To shorten the questionnaire, some pathologies for which clinical signs may overlap were combined. For instance, inappropriate toileting and marking may both result in urination outside of the litter box, and cats with either territorial aggression or inappropriate play behavior may stalk or ambush other household cats, without displaying distance-increasing vocalizations. See the Supplementary Materials (Item C) for a list of questions used to identify each pathology. For simplicity's sake, a subject was considered to exhibit a pathology if an answer other than "never" was returned for any of the contributing questions.

Data collection

The Fe-BARQ, modified as described to collect information about clinical behavior pathologies and physical appearance, was established as an open-access, online survey. The link to this survey was disseminated to the members of the World Cat Congress, which comprises The International Cat Association, the WCF, the CFA, and 4 additional international registries. These registries were asked to share the survey link with their members. In addition, the survey was promoted on social media (Facebook). Participants were asked to

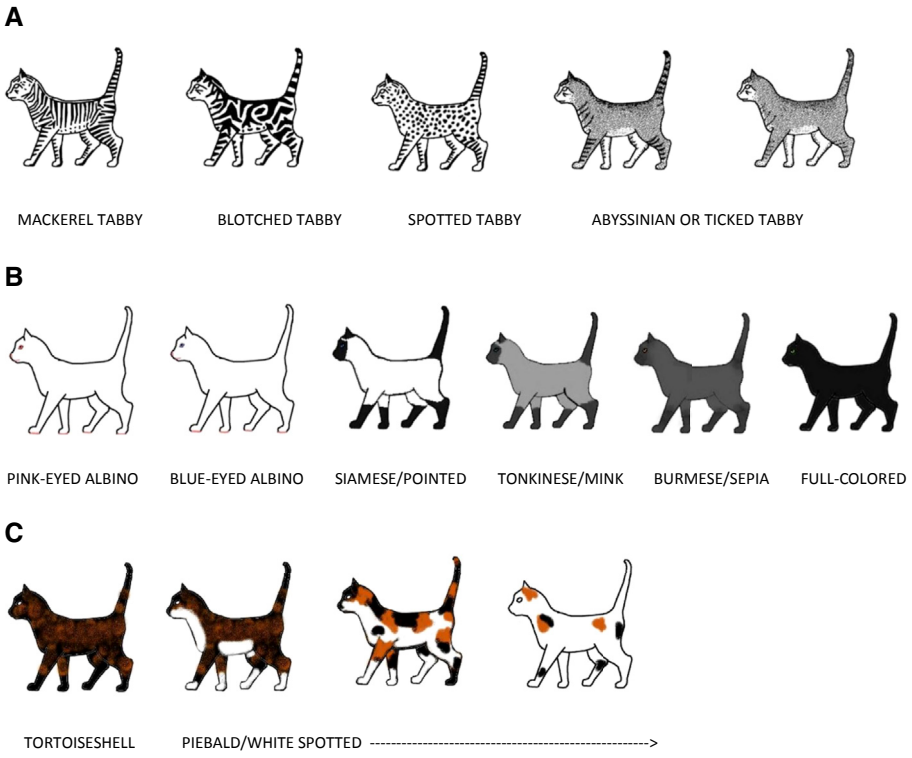

Figure 1. Genetically distinct coat patterns in domestic cats. (A) Mackerel, blotched, spotted, and ticked patterns represent allelic variation at the tabby locus. Homozygosity for the recessive nonagouti (a) modifier gene results in a "self-colored" or solid coat. (B) Pink-eyed albino, blue-eyed albino, Siamese or pointed, Burmese or sepia, and Tonkinese or mink patterns represent allelic variation at the albino locus. Dominant full-colored or traditional coat (C) included for comparison. (C) Tortoiseshell coat pattern results from heterozygosity at the sex-linked orange locus. In cats with at least 1 incompletely dominant *S* allele at the white spotting locus, varying degrees of piebaldness occur. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.) Images modified from Sarah Hartwell (messybeast.com) with permission.

complete the survey only for registered, single-breed cats, and to cite the registry or registries to which each cat belonged. Each participant was permitted to complete the survey for up to 3 cats in his or her household. Selection from the cats in a multicat household was to be made in alphabetic order, beginning with the cat whose call name (the short, pet name used to refer to the cat on an everyday basis) fell closest to the beginning of the alphabet. Participants were requested to have all subject cats' pedigrees available when completing the survey, for purposes of coat color and pattern identification. Participants were informed that survey completion would require approximately 30 minutes, and contact information in the event of questions or concerns was provided at the conclusion of the survey.

Statistical analysis

The data were not normally distributed (D'Agostino et al., 1990; Royston, 1991), so a 2-sample Wilcoxon rank-sum (Mann-Whitney) test was used to look for associations between Fe-BARQ factor scores and breed, coat color, eye color, and 2-allele coat patterns. Subjects were categorized as members or nonmembers of each breed and phenotype (i.e., black cats and cats of all other colors, piebald cats and non-piebald cats, or Abyssinian cats and cats of all other breeds). The Kruskal-Wallis equality of populations rank test was used to detect the presence of a significant association between Fe-BARQ factor score and any coat pattern associated with a multiallele trait (i.e., tabby patterning). If such an association was found, Dunn's pairwise comparison (with Bonferroni correction) was used to determine which pattern or allele was responsible for this significance. Fisher's exact test was used to identify significant associations between the presence of a behavior pathology and breed, coat color, eye color, and coat pattern. If a significant association was discovered between behavior and physical appearance, logistic regression was used to ascertain whether this significance was due to the breed of the subjects with that phenotype. Significance was set a priori as $P < 0.05$. Only breeds for which at least 15 representatives were available were included in the analysis.

Results

Population characteristics

Surveys were completed for 574 cats. Partially completed surveys (913) were excluded from the study. Subject cats resided in 23 countries, with half (50%; N = 285) living in the United States. Females (48%; N = 273) and males (52%; N = 301) were equally represented. Most cats (79%; N = 451) were neutered but not declawed (96%; N = 550). Although 71% (N = 405) of cats had been obtained from a breeding cattery, the majority currently lived in a house, apartment, or condo (85%; N = 488). Approximately 85% (N = 473) of the cats in the study lived in multicat households. Twenty-four cats were excluded because of failure to list a recognized registry. For the remaining subjects, the breeds with at least 15 representatives included Abyssinians, Bengals, Birmans, Burmese, Devon rexes, Maine coons, Norwegian Forest cats, Orientals, Persians, Ragdolls, Siamese, and Tonkinese. One hundred fifty-six cats not belonging to these breeds were excluded from statistical analysis. The final number of surveys included in the analysis was 394.

Associations between breed and behavior

Multiple statistically significant associations were found between breed and Fe-BARQ factor scores and between breed and

the presence of behavior pathologies. For an illustration of the variation in Fe-BARQ scores among breeds, see Figure 2. For more populous breeds, more significant associations were identified. Associations were internally consistent within a breed, which may be suggestive of a "personality profile" for that breed. For instance, Abyssinians were found to display increased Fe-BARQ scores for sociability (with people) and cat aggression. Abyssinians also had decreased scores for restraint resistance and vocalization, and a reduced likelihood of fear of noises. Birmans exhibited decreased Fe-BARQ scores for activity/playfulness, vocalization, trainability, and predatory behavior, and were more likely to exhibit fear-related aggression (toward familiar people) and inappropriate elimination.

Fe-BARQ scores for attention seeking, separation-related behavior, and sleeping in elevated/warm/hidden locations were decreased for Maine coons, the most populous breed in this study. Separation anxiety and inappropriate elimination were also less likely to occur in Maine coons, but they had increased scores for owner-directed aggression and prey interest. Tonkinese cats, the second most populous breed in this study, had increased Fe-BARQ scores for playfulness, sociability (with people), vocalization, attention seeking, separation-related behavior, and trainability, and decreased scores for owner-directed aggression, restraint resistance, and cat aggression. Tonkinese were also less likely to manifest fear-related aggression toward familiar cats. See Table 1 for a comprehensive listing of associations between breed and behavior.

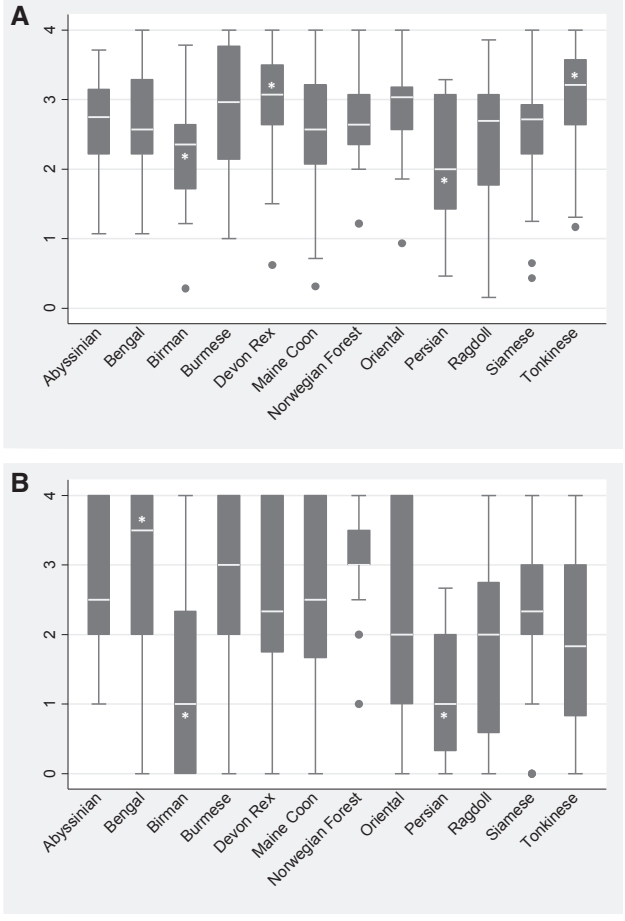

Figure 2. Comparison of Fe-BARQ scores among breeds with greater than 15 representatives. An asterisk denotes significance. (A) Birmans and Persians demonstrated significantly lower scores for playfulness than cats not of those breeds, whereas Devon rexes and Tonkinese demonstrated significantly higher scores. (B) Birmans and Persians demonstrated significantly lower scores for predatory behavior than cats not of those breeds, whereas Bengals demonstrated significantly higher scores.

Associations between appearance and behavior

Some associations were found between Fe-BARQ scores and coat color, coat pattern, and eye color. Associations were also found between physical appearance and the presence of behavior problems as identified by the pathology screen. Lilac-coated cats displayed a decreased score for prey interest but increased scores for playfulness, attention seeking, and separation-related behavior. Red-coated cats were more likely to exhibit fear-related aggression toward unfamiliar people and had an increased Fe-BARQ score for prey interest. Piebaldness was associated with a decreased Fe-BARQ score for vocalization and for stranger-directed aggression. The tortoiseshell coat pattern was associated with increased Fe-BARQ scores for cat aggression and prey interest but decreased aggression to dogs.

However, when logistic regression was performed to control for the breed of cats with a given color or pattern, most associations between appearance and behavior were attributable to breed. For instance, lilac-coated Tonkinese had significantly higher playfulness and attention seeking scores than non–lilac-coated non-Tonkinese, but lilac-coated non-Tonkinese did not have higher playfulness and attention-seeking scores. Piebald Birmans had a significantly lower vocalization score than nonpiebald non-Birmans, but piebald non-Birmans did not have lower vocalization scores. In almost all other cases, significant associations between appearance and behavior were lost if at least one breed was excluded from the population.

A limited number of notable exceptions were identified for which breed did not account for the association between physical appearance and behavior. Red Maine coons and non-red Persians were heavily represented in the increased prey interest score found in red-coated cats, but this score was increased even when both breeds were excluded. Persians without Burmese or mink-patterned coats exhibited significantly decreased playfulness relative to full-colored or traditional non-Persians, but Burmese patterned non-Persians still displayed significantly increased playfulness. Lilac-coated non-Tonkinese had a significantly higher Fe-BARQ score for separation-related behavior than non–lilac-coated non-Tonkinese, but lilac-coated Tonkinese did not have a significantly higher score for separation-related behavior (Figure 3). See Table 2 for a comprehensive listing of associations between appearance and behavior.

Discussion

Experts (veterinarians and cat show judges) have been reported to perceive differences in the behavior of distinct breeds of domestic cat (Mendl & Harcourt, 2000; Hart et al., 2013), and cat owners report that color (black, white, orange, bicolored, and tricolored) affects personality traits (Delgado et al., 2012). Owners were more likely to describe orange cats as friendly, tricolored cats as intolerant, and white cats as aloof. We tested the hypotheses that significant associations are present between breed and behavior in domestic cats, and between behavior and coat color, coat pattern, and eye color. These hypotheses were substantiated, and significant associations were identified between behavior assessed by Fe-BARQ and the behavior pathology screen, and all of the aforementioned parameters. However, our hypothesis that associations between appearance and behavior would occur independent of breed was largely unsubstantiated.

Many of our study's findings with respect to breed are congruous with published results. Veterinarians in 2 independent studies characterized Persians as less active, and owners described Persians as less playful and active than Siamese (Mendl & Harcourt,

Table 1
Behavioral associations with breed

Breed (no. of representatives)	Increased/more likely		Decreased/less likely	
	Factor	*P* value	Factor	*P* value
Abyssinian (16)	Sociability (people)	0.02	Restraint resistance	0.01
	Cat aggression	0.03	Fear of noises[a]	0.006[a]
			Vocalization	0.003
Bengal (27)	Predatory behavior	0.03	None	None
	Inappropriate elimination[a]	0.001[a]		
	Inappropriate elimination[b]	0.005[b]		
Birman (40)	Fear-related aggression (familiar people)[a]	0.02[a]	Playfulness	0.0003
	Inappropriate elimination[a]	0.02[a]	Vocalization	0.002
			Trainability	0.02
			Predatory behavior	0.001
Burmese (42)	Dog aggression	0.01	None	None
	Prey interest	0.03		
	Sleeping in elevated/warm/hidden locations	0.002		
	Separation anxiety[a]	0.02[a]		
Devon Rex (37)	Playfulness	0.02	None	None
	Sociability (people)	0.01		
	Sleeping in elevated/warm/hidden locations	0.01		
Maine Coon (71)	Owner-directed aggression	0.02	Attention seeking	0.04
	Prey interest	<0.0001	Separation anxiety[a]	0.002[a]
			Separation-related behavior	0.03
			Sleeping in elevated/warm/hidden locations	<0.0001
			Inappropriate elimination[a]	0.01[a]
Norwegian Forest (17)	None	None	None	None
Oriental (16)	Cat aggression	0.04	None	None
	Compulsive (nongrooming) behaviors	0.02		
	Redirected aggression[a]	0.008[a]		
Persian (15)	None	None	Playfulness	0.03
			Predatory behavior	0.006
			Prey interest	0.01
			Fear-related aggression (familiar cats)[a]	0.03[a]
Ragdoll (37)	None	None	Attention seeking	0.001
			Trainability	0.03
			Sleeping in elevated/warm/hidden locations	0.009
Siamese (29)	Stranger-directed aggression	0.04	Sociability (people)	0.01
			Fear-related aggression (familiar people)[a]	0.02[a]
Tonkinese (47)	Playfulness	0.0005	Owner-directed aggression	0.02
	Sociability (people)	0.01	Restraint resistance	0.03
	Vocalization	0.01	Cat aggression	0.0009
	Attention seeking	<0.0001	Fear-related aggression (familiar cats)[a]	0.001[a]
	Separation-related behavior	0.01		
	Trainability	0.02		

[a] Pathology screen.
[b] Fe-BARQ score.

2000; Hart et al., 2013). Here, Persians were distinguished by decreased Fe-BARQ scores for activity/playfulness, predatory behavior, and prey interest. Bengals, previously described as most likely to urine mark (Hart et al., 2013), were characterized by a significantly increased Fe-BARQ score for inappropriate elimination and a significantly increased likelihood of inappropriate elimination on the behavior pathology screen.

Although the results of our study were most often consistent with previous studies, some inconsistencies were found. Siamese cats have been reported to exhibit increased vocalization and interaction with owners (Mendl & Harcourt, 2000), a conclusion not supported by our data. It is possible that subpopulations of cats vary considerably, and that the behavioral patterns of a population may change with time and breed popularity.

Associations were found to exist between behavior and coat color, coat pattern, and eye color, but our hypothesis that these associations would be independent of breed was not strongly supported. Most of the behavioral associations with coat color and pattern could be attributed to the breed of the animals with those colors and patterns. A limited number of breed-independent associations were discovered and can be seen as concordant with previous data.

Red British shorthair kittens exhibited increased restraint resistance and latency to quieting compared to kittens of other colors (Mendl & Harcourt, 2000). In our study, red cats exhibited an increased likelihood of fear-related aggression toward unfamiliar people, independent of breed. Both of these observations may be considered consistent with an increased tendency toward stress, or with a proactive coping strategy when stressed. A similar conclusion may be drawn with respect to agouti coat color where we found an association with increased Fe-BARQ score for cat aggression. Enhanced agouti protein expression in the murine CNS is associated with an increased stress response and corticosterone production (Harris et al., 2001).

Piebald cats exhibited decreased stranger-directed aggression, a finding consistent with the observation that foxes selected for decreased aggressiveness to humans had increased white spotting (Trut et al., 2004). Mutations within the murine white spotting (W) locus have pleiotropic effects on embryogenesis (Geissler et al., 1988). Expression during late gestation affects both melanoblasts and the CNS, which may influence behavioral development (Orr-Urtreger et al., 1990).

We found that red cats had increased prey interest independent of breed, as evaluated by the Fe-BARQ. This finding may make sense in the context that red cats represent a larger percentage of the population in rural environments (Pontier et al., 1997) where feral or semiferal cats still subsist on small prey (MacDonald et al., 2000).

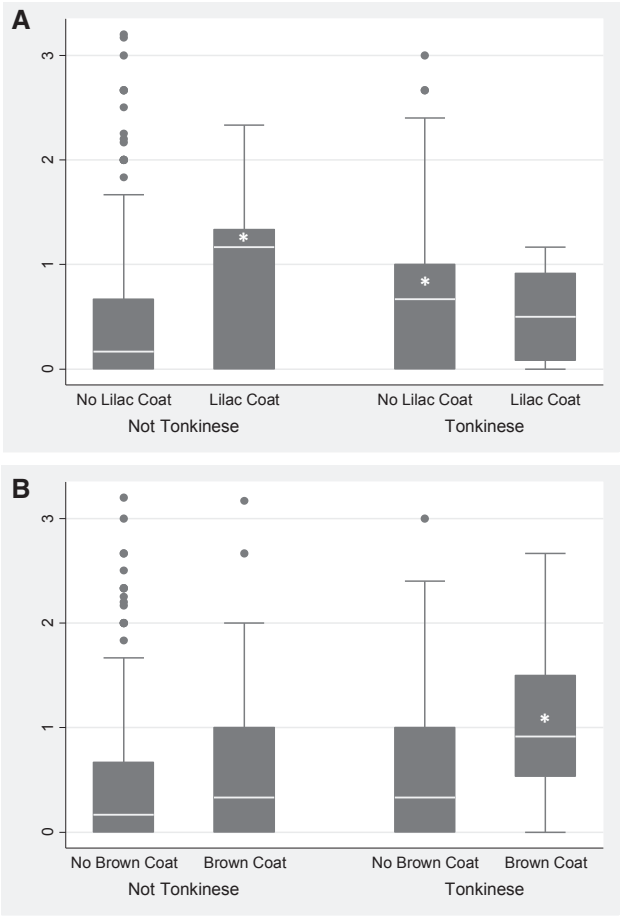

Figure 3. (A) A limited number of breed-independent associations between behavior and physical appearance were discovered, as exemplified in these box-and-whisker plots. Lilac-coated non-Tonkinese had a significantly higher Fe-BARQ score for separation-related behavior than non–lilac-coated non-Tonkinese, but lilac-coated Tonkinese did not. (B) Many associations discovered between behavior and physical appearance could be attributed to the breed of the subjects with that phenotype. For instance, brown-coated Tonkinese had a significantly higher Fe-BARQ score for separation-related behavior than non–brown-coated non-Tonkinese, but brown-coated non-Tonkinese did not. An asterisk denotes significance.

Interestingly, significantly increased Fe-BARQ scores for separation-related behavior or an increased incidence of separation anxiety as a behavior pathology was seen in cats lacking the dominant allele for a full-colored or traditional coat pattern. Siamese, Burmese, and Tonkinese patterned individuals were distinguished, independent of breed. Tyrosinase gene expression in the CNS is limited to the retinal pigment epithelium (Gimenez et al., 2003). Mammals with reduced retinal pigment have been shown to develop correspondingly increased cross retinal projections (Kaas, 2005), suggesting that abnormal vision in cats with decreased pigmentation (e.g., Siamese) could result in increased baseline anxiety. It is also possible that the tyrosinase mutations responsible for Siamese, Burmese, and Tonkinese coat patterns cosegregate with alleles responsible for enhanced development of social attachment, but not for elevated baseline stress. Larger, targeted studies are needed to explore such questions.

Overall, the paucity of independent associations between appearance and behavior suggests a low level of pleiotropy, whereby genetic changes (in this case, those artificially selected to produced unique coat colors and patterns) cause changes in more than one phenotypic trait. The low number of associations, independent of breed, between behavior and physical appearance suggests that physical appearance is a not a reliable indicator of personality in the domestic cat. This study may provide information helpful to breeders wishing to improve their reproductive population with respect to breed-specific behavioral characteristics and pathologies.

Table 2
Behavioral associations with coat color, coat pattern, and eye color

	Increased/more likely	*P* value	Decreased/less likely	*P* value
	Factor		Factor	
Coat colors				
Agouti	**Cat aggression**	0.001	None	None
	Predatory behavior	0.03		
Brown	Separation-related behavior	0.003	None	None
Red	**Prey interest**	0.002	None	None
	Fear-related aggression (unfamiliar people)[a]	0.02[a]		
Cinnamon	Sociability (people)	0.04	None	None
Lilac	Playfulness	0.02	Prey interest	0.005
	Attention seeking	0.03		
	Separation-related behavior	0.03		
Fawn	Vocalization	0.03	None	None
Caramel	Vocalization	0.02	None	None
Coat patterns				
Siamese/pointed	**Separation anxiety**[a]	0.02[a]	Predatory behavior	0.009
Burmese/sepia	**Playfulness**	0.02	None	None
	Separation anxiety[a]	0.003[a]		
	Separation-related behavior	0.04		
Tonkinese/mink	Playfulness	0.02	Restraint resistance	0.02
	Separation anxiety[a]	0.03[a]		
	Separation-related behavior	0.02		
Abyssinian/ticked tabby	Cat aggression	0.01	None	None
	Fear-related aggression (familiar cats)[a]	0.03[a]		
Mackeral tabby	Fear-related aggression (familiar cats)[a]	0.05[a]	None	None
Spotted tabby	Inappropriate elimination[a]	0.04[a]	None	None
Blotched tabby	Prey interest	0.03	None	None
Silver/chinchilla/shaded	Cat aggression	0.008	None	None
	Fear-related aggression (familiar cats)[a]	0.03[a]		
Tortoiseshell	Cat aggression	0.04	Dog aggression	0.009
	Prey interest	0.01		
Piebald	None	None	**Stranger-directed aggression**	0.01
			Vocalization	0.01
Eye colors				
Gold (white coat)	None	None	**Fear of noises**[a]	0.04[a]

Bolded entries denote associations independent of breed. All other entries denote associations attributable to breed.
[a] Pathology screen.

Further expansion on this study is indicated. Several limitations were imposed by the study design, population, and data analysis. The study was retrospective in nature, and relied on subjective owner recollection of past events. As a survey-based study, the present work was able to include a large population of single-breed, registered cats, but no independent observer verified owner reports on subject behavior, registry, or physical appearance. Even if participants derived color and pattern classification directly from the subjects' pedigrees, as instructed, these classifications are often determined by a cat's breeder and are not always reviewed by a judge or other official. The survey was disseminated in part using social media which has been reported to result in a significant population bias toward certain age, gender, and socioeconomic brackets (Alshaikh et al., 2014; Valdez et al., 2014).

Cats lacking recognized registries and from breeds with fewer than 15 representatives were excluded to enhance statistical power. The Fe-BARQ and behavior pathology screen used to assess behavior in the study population are not currently validated. The results obtained are intuitive and internally consistent, with some overlap occurring between the results of the Fe-BARQ factor scores and the surveyed behavior pathologies. Ideally, a subsequent step would comprise ethologic evaluation of included breeds by a blinded, independent observer. Multiple single-breed populations with representatives of varying colors and patterns could also be assessed for associations between behavior and physical appearance.

Conclusions

This study identified significant associations between behavior and genetically distinct cat breeds, coat colors, coat patterns, and eye colors. The limited breed-independent associations were concordant with prior studies, suggesting the presence of low level pleiotropy or cosegregation of genes influencing behavior and coat type. However, most associations between behavior and physical appearance could be attributed to breed-based behavior differences. Although further research is required, the unexpected discovery that a population of single-breed cats manifests few breed-independent associations between appearance and behavior is of relevance to our fundamental understanding of feline genetics and ethology.

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Ethical considerations

This research did not involve the use of live vertebrate animals owned by the University or its clients; nor did it involve the acquisition of identifiable private information about human subjects. A page summarizing the study and its purposes preceded the online survey.

Conflict of interest

We have read and understood this journal's policy on declaration of interests and declare that we have no competing interests.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jveb.2016.03.009.

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