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Tell-Tail Fear Behaviors in Kittens: Identifying the Scaredy Cat

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Abstract – Identifying when kittens are in fearful emotional states is crucial to protecting welfare, preventing behavioral issues, and ensuring caretaker and researcher assessments are accurate. Research is needed to confirm if kittens have fully developed fear responses similar to those of adult cats when they are in situations that evoke fear. To assess which behaviors kittens show when they are avoiding novel and startling stimuli, kittens (5 to 8 weeks old; n = 46) completed trials involving exposure to such stimuli, alternating with blank control trials. Trials were separated into immediate responses (during a short stimulus presentation or equivalent control period), and delayed responses (after stimulus removal). Mixed regression models, with litter and kitten as random intercepts, were used to model durations and frequencies of behaviors. Across both time phases, kittens displayed significantly longer durations of arched back, piloerection, freezing, and tail tucking, shorter durations of eating, and greater rates of putting their ears back during fear trials compared to blank trials. During stimulus presentations, kittens displayed significantly shorter durations of retreating to a hutch and greater rates of flinching, whereas after stimulus removal, kittens displayed significantly longer durations of crouching and shorter durations of upright tail. Responses were also affected by kitten coat color, sex, and being mother-reared. Thus, fear behaviors in 5-to-8-week-old kittens are fully developed and similar to what is observed in adult cats. These results allow for accurate identification of fear in kittens, with the goal of improving research on kitten fear development and kitten welfare.

Keywords – Kitten, Fear, Behavior, Socialization, Coat color, Mother-reared

It is generally assumed that kittens (*Felis silvestris catus*) show the same fear responses as adult cats (Kolb & Nonneman, 1975); however, there are few studies on this topic leaving the possibility that kitten responses differ from adult cats or are not fully developed. Fear is an emotion that serves as an intervening variable between a perceived or real threat and a suite of behavioral responses meant to allow the individual to cope with the threat (Adolphs, 2013). The state of fear can be considered a protective (negative) emotion with a goal of increasing survival (Panksepp, 1998; Rodan et al., 2022). Ongoing fear is also a welfare concern as it can lead to health (e.g., Griffin, 1989) and behavioral issues (e.g., Levine, 2008). If caretakers cannot correctly identify when their kittens are in a state of fear, they might continually put kittens in fear-provoking conditions. Importantly, fear in cats can progress to behavioral issues such as aggression (Levine, 2008), which can further impact welfare, reduce the human-animal bond, and lead to mistreatment, relinquishment to shelters, and/or euthanasia (DiGiacomo, Arluke, & Patronek, 1998; Salman, New Jr., Scarlett, & Kris, 1998; Salman et al., 2000). Given this impact on animal welfare, it is critical that we properly identify fear in kittens, both to aid in its management and prevention and to improve research on this important topic.

It is particularly important to accurately recognize fear in kittens when they are young because of the critical role of early life experiences on the development of the brain, behavior, and health. Like many animals, kittens have a sensitive period for development in which the brain shows enhanced plasticity for learning about the social and physical world around them (Knudsen, 2004). In kittens, the sensitive period for socialization occurs between approximately 2 and 9 weeks of age (American Veterinary Medical Association, 2015; Bateson, 2014; Karsh, 1984; Karsh & Turner, 1988; Lowe & Bradshaw, 2001). Inadequate or negative early experiences, such as being exposed to maternal or social deprivation, malnourishment, or ongoing stress, can lead to heightened fearfulness and anxiety, aggression, reactive stress physiology, disturbed neural functioning, changes in immunity, and stereotypic behavior (Latham & Mason, 2008; Levine, 2008; Stevens et al., 2009). Appropriate early exposure and habituation to potentially fear-provoking stimuli (e.g., positive encounters with unfamiliar humans and animals, new environments, loud noises) during this period can help provide familiarity and mitigate fearful responses to such stimuli over an animal's life (American Veterinary Medical Association, 2015; Lowe & Bradshaw, 2001; Serpell et al., 2016). The socialization period is therefore a crucial time to instill long-term well-being. However, exposure to such stimuli needs to be species-specific and tailored to the individual and their stage of development, and exaggerated signs of fear need to be recognized early and avoided to protect against potential negative impacts (Mendl & Harcourt, 1988). Ideally, exposure should be a neutral or positive experience, and paired with positive rewards or encouragement, such as food or treats (i.e., counterconditioning), to reduce the likelihood of the kitten making negative associations that could have lasting effects (Levine, 2008).

Previous research has investigated and identified various fear behaviors in adult cats. In one study, defensive behavior was chemically induced in test cats using an injection of carbachol, and these cats were then exposed to a second cat who was electrically stimulated to emit threatening behavior (Johansson et al., 1979). In this context the test cats responded with increased withdrawal (i.e., avoidance), a crouched body position, drawing back of the ears, and hissing. Other behaviors indicative of fear that have been observed in adult cats in other studies include tucking their tail between the hind legs or wrapping their tail tightly around the body or hind legs, attempting to escape, forward facing whiskers, wide eyes, and dilated pupils (Bradshaw et al., 2012; Kessler & Turner, 1997; Roberts, 1958). Further, based on observational studies, Leyhausen (1979) has outlined a gradient of facial expressions and body postures that align with the behaviors described above and which are representative of increasing fear and defensive or aggressive behavior patterns in adult cats.

While fear responses in adult cats have been well described, more research is needed to determine if kittens share similar patterns, where the complete repertoire of fear behaviors might not be fully developed. One study looked at responses of both kittens and adult cats in the same experiment and found that 6-week-old kittens display similar arched back behavior and piloerection (when the fur on the back and tail are puffed up) as adult cats in response to a threatening visual stimulus (i.e., a silhouette of an adult cat; Kolb & Nonneman, 1975). However, other behavioral responses in kittens, and kitten responses to other types of stimuli, have not been examined. Studies have found that puppies display the majority of common fear behaviors observed in adult dogs (Flint et al., 2018), and infant laboratory rats display the same fear behaviors in adulthood, though the proportion of time spent engaging in the behaviors decreased with age (Kabitzke & Wiedenmayer, 2011). Similar findings showing the early development of adult-like fear behavior have been observed in horses, cattle, pigs, sheep, and poultry (reviewed in Forkman et al., 2007; Lansade et al., 2008).

Our overall objective was to assess behaviors that are indicative of fear in kittens to improve their identification and reduce potential misclassification of this emotional state. Across the animal kingdom, novel and startling stimuli have been found to induce fear responses, and avoidance is considered to be a key component of a fear response to these stimuli (Adolphs, 2013; McNaughton, 2011). The act of avoidance makes evolutionary sense as a functional response to cope with a threat and to increase the chances of survival. In the current study, we investigated kitten responses to two social stimuli (cat model with growling and hissing; dog model with barking) and one non-social stimulus (hand vacuum pulsed on and off) that were expected to elicit a fear response in kittens based on stimuli salience and previous research. Aggressive feline vocalizations have been found to elicit defensive responses in cats (Adamec et al., 1983), dogs are innate evolutionary predators of cats (reviewed by Bradshaw, 2016), and loud household items, like vacuum cleaners, have been reported to provoke fear in companion cats (e.g., Howell et al., 2016). Therefore, we investigated responses to stimuli representing these fear-provoking contexts using the *a priori* criterion of avoidance to identify concurrently occurring fear behaviors in 5- to 8-week-old kittens. We hypothesized that kittens of this age, who are mobile and interacting with social partners and the environment, would have a fully developed fear response, which predicts that they would show a similar fear behavioral repertoire to adult cats. We also expected that kitten responses would be impacted by particular kitten characteristics, such as coat color or maternal status. We examined differences between mother-reared and orphaned kittens because early separation has been shown to impact stress behaviors in young kittens, with orphaned kittens being more responsive (e.g., Lowell et al., 2020). Additionally, we investigated the following: kitten coat color, which has been found to have varying associations with cat behavior (reviewed by González-Ramírez and Landero-Hernández, 2022); sex, which has been found to influence behavior in other species, such as dogs (reviewed by Gartner, 2015); and litter size, which has been found to influence behaviors such as play and aggression in cats, with single kittens experiencing less social play than kittens with siblings, and single-kitten mothers showing higher levels of aggression than mothers of two kittens (Mendl, 1988).

Materials and Methods

Ethics Statement

This research was approved by the University of Guelph's Animal Care Committee (AUP#3943) and conformed to all federal and provincial guidelines governing the use of animals in research. All kittens remained under the care of the Guelph Humane Society and were adopted shortly following testing.

Animals

Kittens (n = 46; estimated ages from 5 to 8 weeks old) from 13 litters were recruited through the Guelph Humane Society (Guelph, Ontario, Canada). This age range was selected because it is within the socialization window for kittens, follows weaning and sufficient development of sensory and motor systems for performance of behavioral responses, and is prior to sterilization and adoption (e.g., American Veterinary Medical Association, 2015). All kittens were foster housed with volunteer community members in the litters within which they were brought to the shelter and were homed with their mother if she was available. Sex, presence of the mother, litter size, and coat color of each kitten were recorded. Coat color was determined by the experimenter and recorded as the majority color of the kitten's fur (e.g., if a kitten was mostly black with white paws and/or a white tuft, coat color was marked as "black"). "White" included all white, and mostly white (e.g., primarily white with black or gray patches), "tabby" included gray, brown, and orange tabby coats, and "tri-color" included calico and tortoiseshell coats. Final coat color categories were "black," "gray," "white," "tabby," and "tri-color."

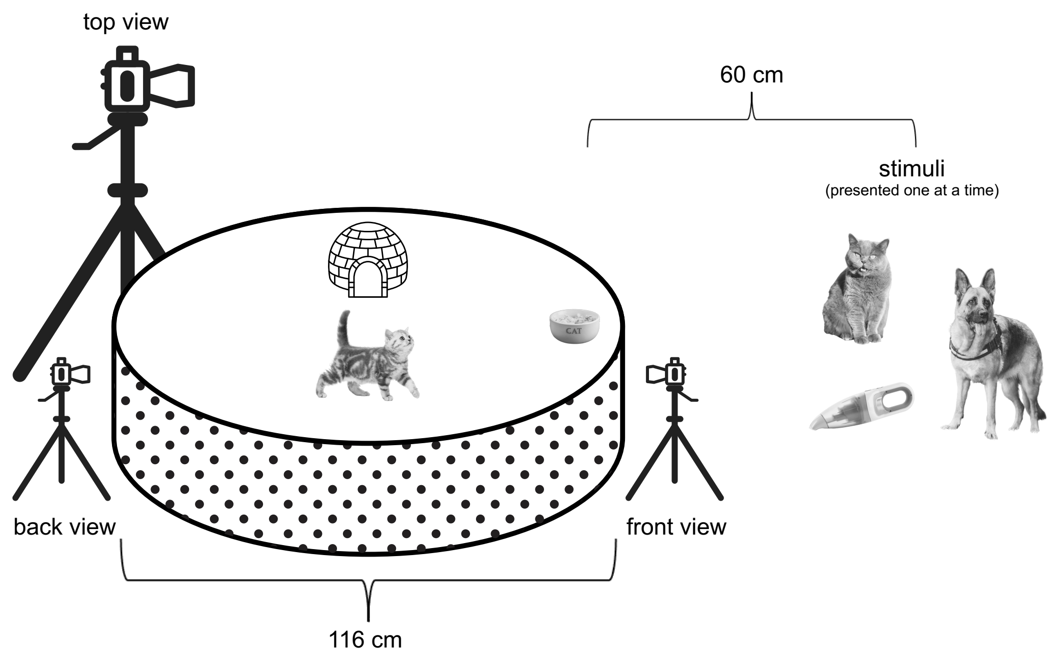
Behavior Testing

Equipment Setup

All behavior tests were conducted in the kittens' foster homes within a hexagonal mesh soft-sided pet exercise pen (116 cm on each side x 71 cm high; Petmate®, Doskocil Manufacturing Company Inc., Arlington, Texas, USA). Inside of the pen, we placed a semi-transparent plastic hutch (40 cm x 35 cm x 20 cm, Kaytee Products Inc., Chilton, Wisconsin, USA) for retreat on one side and the kittens' own food dish on the other side (Figure 1). During testing, kittens were provided with Royal Canin Instinctive Kitten wet food (Royal Canin, St. Charles, Montana, USA) mixed with KMR® Kitten Milk Replacer Powder (Pet-Ag Inc., Hampshire, Illinois, USA) to provide a distraction and palatable treat; all kittens had prior experience with the food and KMR. All behavior tests were video recorded with three video cameras (Sony HDR-CX330 9.2 Megapixels Handycam, Sony Corp., Tokyo, Japan): one attached to a tall tripod (Manfrotto M190X, Cassola, Italy) providing a top view of the pen, and two attached to gorilla pods (JOBY, The Vitec Group, Petaluma, California, USA) providing front and back views at kitten level.

Figure 1

Schematic of Equipment Setup for Kitten Behavior Assessments



Note. Social stimuli were plush replicates of a cat and dog paired with audio recordings of cats growling and dogs barking, respectively. The non-social stimulus was a small hand vacuum pulsed on and off. Each stimulus was presented one at a time for 10 seconds. Schematic created in Canva Premium graphic design platform (Australia).

Testing Procedure

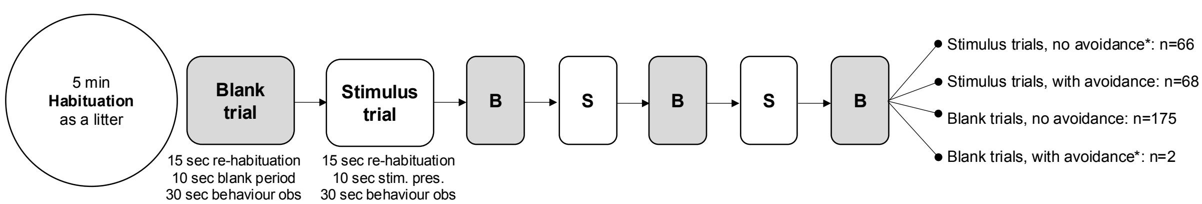
Stimuli. We exposed kittens to two social stimuli and one non-social stimulus. Social stimuli included a plush gray cat (approximately 48 cm x 25 cm x 18 cm, Ty®, Oak Brook, Illinois, USA) and a plush German shepherd dog (approximately 76 cm x 30 cm x 53 cm, Melissa & Doug LLC, Wilton, Connecticut, USA). Ten-second audio clips to accompany each visual stimulus were created by mixing YouTube videos of cats meowing and hissing, and dogs barking and growling (made in iMovie for Mac, version 10.1.8, Apple Inc.), and were used in conjunction with the plush cat and dog presentations, respectively. A small wireless speaker (7.5 cm^3, ZENBRE F3 6W, ZENBRE Corp., London, UK) was connected by Bluetooth to the researcher's (CG) iPhone to play the audio clips through the Music application and placed beside the front facing video camera. The non-social stimulus was a hand vacuum (30 cm x 20 cm x 14 cm, Black & Decker Dustbuster, Towson, Maryland, USA) that was pulsed on and off for 10 sec (5 pulses) and placed beside the front facing video camera. The volume of all stimuli was tested using the Decibel X app for iPhone (V7.0.0, SkyPaw Co. Ltd, Hanoi, Vietnam) to ensure sound levels were similar across stimuli (cat: 73.2 dB, dog: 73.9 dB, vacuum: 73.3 dB; audio clips available in Table S1 in Supplemental Material). A research assistant was hidden behind a cardboard screen with just their hand reaching out holding the stimuli and moving the dog or cat to mimic natural movements; the vacuum was held stationary while pulsed off and on. The assistant was kept out of sight from the kitten to avoid any human association with the stimuli.

Habituation. At each foster home, kittens were placed as a litter in the center of the exercise pen by either the foster caretaker or the experimenter to allow for habituation to the pen for a period of five minutes. All kittens were then removed to a separate and familiar room where they were out of visual and audible range of the testing area.

Exposure Trials. Following habituation, kittens were brought to the experimental room one at a time by the foster caretaker. Each trial commenced once the foster caretaker placed the kitten into the pen. Once a kitten was placed in the pen, each trial included 15 seconds for re-habituation, then 10 seconds of no intervention (for blank trials) or 10 seconds of stimulus presentation (for stimulus trials), followed by 30 seconds of behavior observation (Figure 2). The kitten was then picked up by the foster caretaker and given 10 to 15 seconds of gentle petting for comfort before being placed back in the pen for the next trial. This process was repeated until all trials were finished, starting and ending with a blank trial, and alternating blank and stimulus trials for a total of 7 trials per kitten. Each session took approximately 10 min for each kitten. The order of stimulus presentation was randomized for each kitten to avoid any temporal bias. If at any point a kitten showed extreme fear or attempts to escape (i.e., climbing up the pen wall, jumping out of the pen), they were immediately removed from the pen and the trial was terminated. In this case, kittens were picked up and gently petted by the foster caretaker and given a break from the study. After a period of time (approximately 1 to 5 min), if the kitten was sufficiently calm (as deemed by the foster caretaker), they were placed into the pen again to proceed with the subsequent trial. Trials that were terminated without successful reattempts were not included in analyses (n=8 [2.57%] from six kittens who had no obvious identifying characteristics).

Figure 2

Flowchart of Behavior Assessment



Note. Habituation was conducted as a litter, after which each kitten was assessed individually. Each individual trial began with a blank control trial, was alternated with a stimulus trial, and ended with a blank control trial. Stimuli were presented one at a time and the order of presentation was randomized for each kitten. * = removed from analyses to ensure fear trials included avoidance and non-fear trials did not.

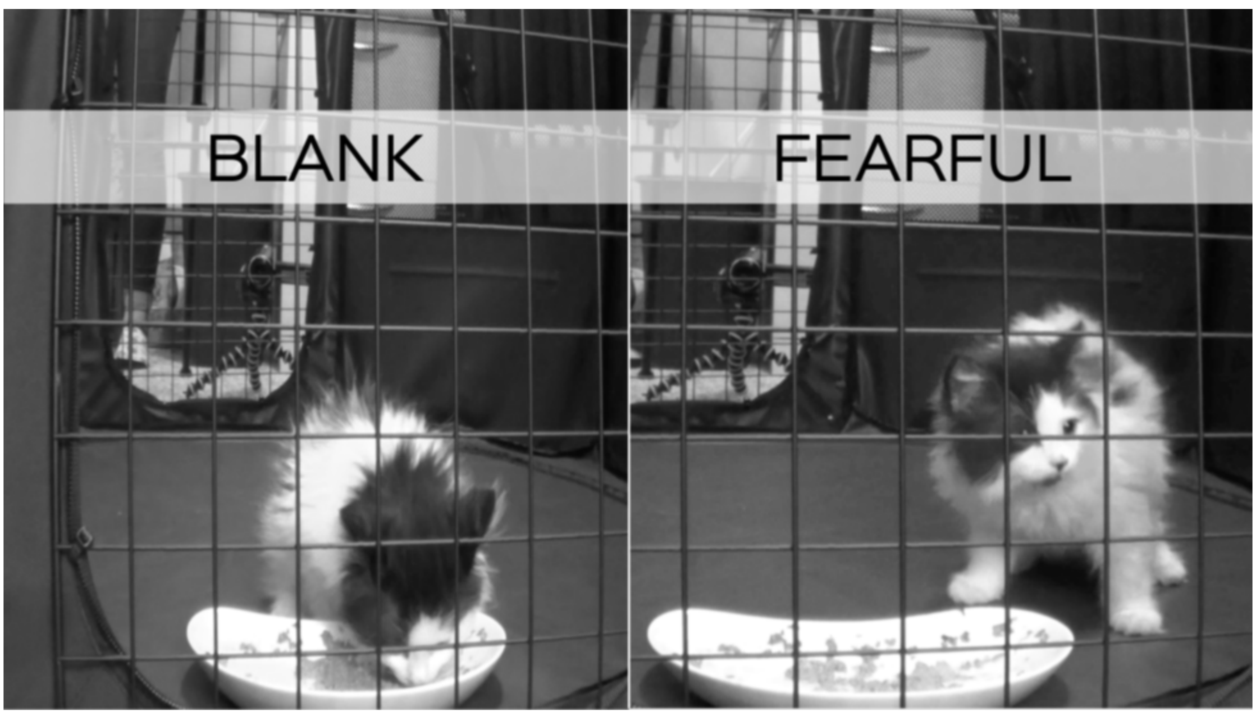
Video Scoring

Using the *a priori* criterion of avoidance (a known fear response; e.g., Adolphs, 2013), trials where kittens were exposed to novel stimuli—and showed avoidance—were labelled as fear trials and were compared to blank trials without stimuli present—and without avoidance (Figure 3; see also Figures S1a and S1b in Supplemental Material for example videos of trials). Avoidance was defined as the kitten retreating away from the area of stimulus presentation at any point during the trial, including retreating to the back end of the enclosure or moving away from the stimulus. Any occurrences of avoidance during blank trials may have resulted from fear in response to some other aspect of testing or the environment, and not from the stimuli being assessed, and were therefore removed from analyses to ensure blank trials properly represented a "no fear" condition (n = 2).

Videos of all trials were scored in randomized order by a single observer (SK) using The Observer XT 12 software (Noldus Information Technology, Netherlands). Due to the sound of the stimulus presentations (i.e., meowing, barking, or vacuum pulses), it was not possible to completely blind the observer to whether trials were stimulus or blank trials as volume was needed to score vocalizations; however, the observer was blind to study hypotheses and objectives to reduce bias, but was aware of condition (i.e., cat, dog, vacuum, or no stimulus). The observer also underwent extensive training of kitten behaviors using an ethogram of behaviors that have previously been associated with fear in adult cats and other animals, including body, tail, and ear positions, lip licking, freezing, piloerection, paw lifting, flinching, and vocalizations (i.e., hissing, growling, meowing) (Table 1; Bradshaw et al., 2012; Delgado et al., 1954; Fernandez de Molina and Hunsperger, 1959; Johansson et al., 1979; Kaada et al., 1953; Mason, 2000). Training included reviewing the ethogram in detail, with video and photo examples. State behaviors were recorded as the duration of time spent performing the behavior (in seconds), while point behaviors were recorded as frequencies. For facial behaviors, the time the kitten's face was visible in the video (in any of the three angles captured: front, back, top) was used as the denominator.

Figure 3

Example Video Stills from Footage of Blank (Control) and Fearful (Test) Trials



Note. Video stills from a blank control trial (left) and a stimulus trial classified as fearful (right) during a behavioral test assessing the presence of particular feline fear behaviors in young kittens in response to novel social and non-social stimuli. See also Figures S1a and S1b in Supplemental Material for example videos of trials.

Table 1

Ethogram of Kitten Behaviors Scored During a Behavioral Test Assessing the Presence of Feline Fear Behaviors in Kittens in Response to Novel Social and Non-Social Stimuli

Behavior	Description	Type
POSTURES		
Arched back	Kitten curves their back arched upwards and stands rigidly	State
Crouching	Kitten positions body close to the ground, all 4 legs are bent, belly is touching (or raised slightly off) the ground (*not when crouching to access food)*	State
Piloerection	Kitten raises the fur on the nape of their neck, shoulder, back, and/or tail, giving a puffed-out appearance	State
LOCOMOTION		
Freezing	Kitten suddenly becomes immobile with body tensed for at least 2 sec	State
Slow walking	Kitten is walking slowly *(more cowered and slower than normal walking)*	State
Time in hutch	Kitten is behind or inside of hutch	State
Avoidance	Kitten backs up or runs away from stimulus	State
TAIL		
Upright tail	Tail is upright, held above the line of back	State
Tucked tail	Tail is tucked under or wrapped around the body, held below line of back	State
Tail lash	Kitten moves their whole tail rapidly to one side, or from side to side	Point
HEAD		
Eating	Kitten is eating from food dish; ingests food by chewing with the teeth and swallowing	State
Lip licking	Portion of the tongue is visible and moved along upper lip *(not when eating)*	Point
Face visible	Any time kitten's full face is in view	State
BODY		
Flinching	Kitten suddenly jumps or jolts	Point
Paw lifting	Kitten lifts one of their front paws and holds for at least 1 sec	Point
EARS		
Ears back	One or both ears are turned backwards or sideways	Point
VOCALIZATIONS		
Meowing	A "mew" or "miaou" *(typical meow sound)*	Point
Growling	A low-pitched, throaty, rumbling noise produced while the mouth is closed	Point
Hissing	A drawn-out, low intensity hissing sound produced from rapid expulsion of air from the kitten's mouth	Point
PHASES (mutually exclusive)		
Stimulus	First 10 sec of 40 sec trial; during stimulus presentation	State
Observation	Last 30 sec of 40 sec trial; after stimulus removal	State

Forty videos (20 blank and 20 stimulus trials) were randomly selected to be re-coded by the observer (SK) to determine intra-observer reliability, and by the lead researcher (CG) to determine inter-observer reliability. Intra- and inter-observer reliabilities were assessed using the built-in reliability calculation tool within The Observer software and considered to be acceptable if their Cohen's kappa values were above 0.8. Reliabilities were examined for each of the 40 videos in their entirety, rather than for individual behaviors. However, if there were discrepancies between scores, the observer and researcher went over in explicit detail the video(s) in question, the ethogram descriptions of the behaviors, and specific examples to ensure all behaviors were well understood and rescored the video(s). Final inter- and intra-observer Cohen's Kappa values were 0.91.

Scored behaviors were compared between blank trials without avoidance (n = 175) and stimulus trials where kittens showed avoidance (i.e., fear trials; n = 68) to determine which behaviors were present or were increased or decreased during fear trials.

Statistical Analysis

Data were analyzed using Stata statistical software (v15.1 for Mac, StataCorp. 2015, College Station, Texas, USA). The occurrence of different behaviors hypothesized to be associated with fear (i.e., during stimulus trials when avoidance was present) were analyzed using mixed linear, Poisson, and negative binomial regression models, and compared to behaviors observed during blank trials with no stimulus present and no avoidance. Litter and kitten were included as random intercepts to account for clustering, as there were multiple kittens per litter and multiple trials per kitten. Independent variables included kitten sex, coat color, litter size, and mother-reared or orphaned status. Trials were split into immediate responses, which were those that occurred during the 10-second stimulus presentation or equivalent blank time period, and delayed responses, which were those that occurred during the 30-second behavior observation period after stimulus removal. Prior to fitting our models, we assessed whether independent variables were highly correlated (i.e., $>|0.70|$) to avoid issues concerning collinearity using Spearman rank, Pearson, or Phi correlation coefficients, depending on the variables—no issues with multicollinearity were found. The assumption of linearity between the dependent variables (log of the rate for Poisson and negative binomial models) and continuous independent variables were graphically assessed using locally weighted regression curves (LOWESS) and by testing the inclusion of a quadratic term in the model. If the relationship was nonlinear and could not be appropriately modeled with the addition of a quadratic term, the continuous variable was categorized.

State behaviors were analyzed using mixed linear regression models with duration of the time spent performing the behavior as the continuous outcome. Point behaviors were analyzed using mixed Poisson regression models. Facial behaviors were analyzed using mixed Poisson regression models with the count of behaviors as the outcome and included the natural log of the amount of time the kitten's face was visible as the offset. Mixed Poisson regression models were tested for overdispersion (when the variance is larger than the mean) by refitting them as mixed negative binomial models. If the overdispersion parameter was significant, based on a likelihood ratio test ($\alpha = .05$), the mixed negative binomial model was reported (Dohoo et al., 2014).

Initially, univariable models were fitted for each independent variable and were considered for inclusion in multivariable models if they met a liberal significance level ($\alpha = .20$; Dohoo et al., 2014). All variables significant in the univariable analyses were included in a main effects model and were removed in a manual backward stepwise fashion. Variables were retained in the multivariable models if they were statistically significant ($\alpha = .05$), were considered an explanatory antecedent or distorter variable (i.e., confounding variable), or were part of a statistically significant interaction ($\alpha = .05$). Confounding variables were identified if they were non-intervening and caused a change of greater than 20% in the coefficient of other statistically significant variables in the model when removed and based on their potential causal relationship with the explanatory variable of interest (Dohoo et al., 2014). Two-way interactions were evaluated among all main effects considered. Carryover effects (i.e., pattern or progression of behavioral responses over trials) were evaluated in additional models to investigate changes over the behavior assessment and to confirm the study design was valid.

Model fit was assessed by graphically evaluating the homoscedasticity and normality of the best linear unbiased predictors (BLUPs). Standardized (linear models) and Pearson (rate models) residuals were also assessed to determine if there were any outlying observations, which were then inspected for recording errors and impact on the model. Finally, variance components were reported for each mixed model (i.e., litter, kitten, and observation level for linear models, and litter and kitten level for rate models) regardless of their magnitude. Variance partition components (VPCs) were estimated from the variance components of the mixed linear regression models.

Results

Forty-six kittens (between approximately 5 and 8 weeks of age) from 13 litters were assessed for their behavioral responses to novel stimuli. The sex ratio of kittens was evenly split between females and males (23:23). Litter sizes ranged from 2 to 5 kittens (average: 4.06). Five of the 13 litters had a mother cat in foster care, whereas eight did not. Forty of the 46 kittens avoided at least one stimulus (16 kittens avoided two stimuli; 6 kittens avoided all three stimuli). Descriptions of the kittens and their responses are included in Table S2.

The *a priori* criterion of avoidance occurred during 2 blank trials and during 68 stimulus trials; however, blank trials with avoidance displayed were removed from the final analyses because no stimuli were present.

Comparing Fear and Blank Trials

Primary Behaviors

Behaviors were compared between blank control trials (with no stimulus present and no avoidance displayed; n = 175) and fear trials (with a stimulus present and with avoidance displayed; n = 68). Responses were split within the trials into two phases: the 10 seconds during stimulus presentation (immediate responses) and the 30 seconds after stimulus removal (delayed responses). Across both phases, kittens displayed longer durations of arched back (effect varied with sex in the stimulus presentation phase and coat color in the phase after stimulus removal), piloerection (effect varied with coat color in the phase after stimulus removal), freezing (effect varied with mother rearing in the stimulus presentation phase), and tucked tail (effect varied with mother rearing in both phases and sex in the stimulus presentation phase), shorter durations of eating, and greater rates of drawing their ears back during fear trials compared to blank trials (Tables 2a–c; 3a–c). In the stimulus presentation phase, kittens also displayed shorter durations of time spent in the hutch (Table 2a) and greater rates of flinching (Table 2c) during fear trials compared to blank trials. In the phase after stimulus removal, kittens displayed significantly longer durations of crouching and significantly shorter durations of upright tail during fear trials compared to blank trials (Table 3a). The significant interactions between trial type and kitten characteristics for arched back, freezing, and tucked tail behavior during the stimulus presentation phase (Table 2b), and for arched back, piloerection, and tucked tail behavior in the phase after stimulus removal (Table 3b) are fully reported in the next section on interaction effects. A summary of all significantly different behaviors between trials is reported in Table 4.

Durations of crouching were not significantly different between trial types in the stimulus presentation phase (Table 2a) and time spent in the hutch and flinching were not significantly different between trial types in the phase after stimulus removal (Tables 3a, 3c). Tail lashing was not observed in the stimulus presentation phase and was not significantly different between trials in the phase after stimulus removal (Table 3a). Slow walking, paw lifting, lip licking, meowing, and growling were not significantly different between trial types in either phase (Tables 2a, 2c, 3a, 3c). The models for hissing would not converge in either phase suggesting this behavior was not observed frequently enough for complete analyses (Tables 2c, 3c).

Interaction Effects for Primary Behaviors

In the stimulus presentation phase (i.e., immediate responses), there were significant interactions for arched back, freezing, and tucked tail behaviors between trial type and kitten characteristics (Tables 2a, b). Notably, during fear trials, female kittens displayed longer durations of arched back and tucked tail compared to male kittens and male kittens did not show a difference in either behavior between trials. Further, mother-reared kittens displayed longer durations of freezing and tucked tail compared to orphaned kittens during fear trials. For additional contrasts, please see Table 2b.

In the phase after stimulus removal (i.e., delayed responses), there were significant interactions for arched back and piloerection between trial type and kitten coat color (Tables 3a, b). Notably, during fear trials, kittens with white coats displayed longer durations of arched back compared to all other coat colors (Table 3b). Additionally, during fear trials, kittens with tri-color coats displayed longer durations of piloerection compared to tabby and black kittens, and kittens with white coats displayed longer durations of piloerection compared to tabby kittens (Table 3b). There was also a significant interaction for tucked tail behavior between trial type and being mother-reared (Table 3a). Notably, during fear trials, mother-reared kittens displayed longer durations of tucked tail compared to orphaned kittens (Table 3b). For additional contrasts, please see Table 3b.

Table 2a

Results from Mixed Linear Regression Models for Responses of Kittens During 10-second Stimulus Presentations (i.e., Immediate Responses) During Fear Trials When Kittens Avoided a Stimulus (n = 68) Compared to Blank Trials (referent; n = 175), Including Random Intercepts for Litter and Kitten[a].

Behavior (sec)	Variable(s) or Interaction term(s)	β	95% CI	P-value
Arched back[b] (interaction: trial*sex)	Blank trial	REFERENT		
	Fear trial	1.65	1.02, 2.28	**< .001**
	Female	REFERENT		
	Male	-0.21	1.02, 2.28	.477
	Blank trial*female	REFERENT		
	Fear trial*male	-1.53	-2.44, -0.62	**.001**
Crouching	Blank trial	REFERENT		
	Fear trial	-0.10	-0.61, 0.41	.699
Piloerection	Blank trial	REFERENT		
	Fear trial	2.25	1.40, 3.10	**< .001**
Freezing[b] (interaction: trial*mother-reared)	Blank trial	REFERENT		
	Fear trial	2.17	0.84, 3.49	**.001**
	Orphaned	REFERENT		
	Mother-reared	-0.71	-1.87, 0.44	.226
	Blank trial*orphaned	REFERENT		
	Fear trial*mother-reared	2.72	0.73, 4.72	**.007**
	Black coat color	REFERENT		
	Gray coat color	1.44	0.15, 2.75	**.032**
	White coat color	0.25	-1.19, 1.69	.735
	Tabby coat color	0.52	-0.67, 1.71	.393
	Tri-color coat color	2.40	0.67, 4.13	**.007**
Slow walking	Blank trial	REFERENT		
	Fear trial	-0.28	-0.70, -0.14	.192
In hutch	Blank trial	REFERENT		
	Fear trial	-0.59	-1.10, -0.09	**.021**
Tucked tail[b] (2 interactions: trial*mother-reared AND trial* sex)	Blank trial	REFERENT		
	Fear trial	1.76	0.51, 3.01	**.006**
	Orphaned	REFERENT		
	Mother-reared	0.01	-0.90, 0.92	.979
	Female	REFERENT		
	Male	-0.50	-1.36, 0.35	.250
	Blank trial*orphaned	REFERENT		
	Fear trial*mother-reared	2.49	0.87, 4.10	**.003**
	Blank trial*female	REFERENT		
	Fear trial*male	-1.85	-3.45, -0.24	**.024**
Upright tail	Blank trial	REFERENT		
	Fear trial	-0.04	-0.52, 0.45	.889
	Black coat color	REFERENT		
	Gray coat color	-1.45	-2.47, -0.38	**.008**
	White coat color	-0.71	-1.84, 0.42	.217
	Tabby coat color	-1.36	-2.32, -0.39	**.006**
	Tri-color coat color	-1.20	-2.45, 0.05	.060
Tail lash	Blank trial	REFERENT		
	Fear trial	No observations		
Eating	Blank trial	REFERENT		
	Fear trial	-1.86	-2.72, -1.01	**< .001**

Note: [a] Random intercept variances for each behavior: *Arched back:* litter level = 0.76 (95% Confidence Interval: 0.28, 2.08), kitten level = 0.16 (0.02. 1.26), observation level = 2.53 (2.08, 3.09); *Crouching*: litter level = $9.44*10^{-16}$ ($4.50*10^{-26}$, $1.98*10^{-5}$); kitten level = 0.73 (0.35, 1.54); observation level = 3.18 (2.61, 3.87); *Piloerection*: litter level = 0.035 ($2.81*10^{-10}$, $4.33*10^{6}$); kitten level = 0.11 ($1.61*10^{-5}$, 731.90); observation level = 9.22 (7.59, 11.19); *Freezing*: litter level = $5.55*10^{-17}$ ($5.96*10^{-28}$, $5.16*10^{-6}$); kitten level = $2.08*10^{-18}$ ($8.35*10^{-25}$, $5.20*10^{-12}$); observation level = 12.38 (10.36, 14.80); *Slow walking*: litter level = 0.06 (0.01, 0.58); kitten level = $3.95*10^{-14}$ (0, NA); observation level = 2.24 (1.87, 2.69); *In hutch*: litter level = $3.86*10^{-18}$ ($1.87*10^{-28}$, $7.97*10^{-8}$); kitten level = $1.29*10^{-20}$ ($1.85*10^{-25}$, $8.96*10^{-16}$); observation level = 3.27 (2.74, 3.91); *Tucked tail*: litter level = 0.05558 ($3.65*10^{-5}$,160.61); kitten level = 0.02 ($9.46*10^{-27}$, $2.53*10^{22}$); observation level = 7.99 (6.56, 9.74); *Upright tail*: litter level = 0.20 (0.01, 3.23); kitten level = 0.65 (0.26, 1.64); observation level = 2.91 (2.38, 3.54); *Tail lash:* NA; *Eating*: litter level = 1.11 (0. 35, 3.48); kitten level = $3.11*10^{-18}$ ($1.84*10^{-24}$, $5.12*10^{-12}$); observation level = 9.11 (7.59, 10.94). [b] Please see Table 2b for the interpretation effects of the interactions.

Table 2b

Contrasts of Selected Combinations of Interacting Variables from Mixed Linear Regression Models Presented in Table 2a

Behavior (sec)	Interaction comparisons	β	95% CI	P-value
Arched back (interaction: trial*sex)	Blank trial*male vs. Blank trial*female	-0.21	-0.80, 0.38	.477
	Fear trial*male vs. Blank trial*male	0.12	-0.54, 0.77	.721
	Fear trial*female vs. Blank trial*female	1.65	1.02, 2.28	**< .001**
	Fear trial*female vs. Blank trial*male	1.86	1.14, 2.59	**< .001**
	Fear trial*male vs. Blank trial*female	-0.09	-0.83, 0.64	.801
	Fear trial*male vs. Fear trial*female	-1.74	-2.59, -0.90	**< .001**
Freezing (interaction: trial*mother-reared)	Blank trial*mother-reared vs. Blank trial*orphaned	-0.71	-1.87, 0.44	.226
	Fear trial*mother-reared vs. Blank trial*orphaned	4.18	2.69, 5.66	**< .001**
	Fear trial*mother-reared vs. Blank trial*mother-reared	4.89	3.39, 6.39	**< .001**
	Fear trial*orphaned vs. Blank trial*orphaned	2.17	0.84, 3.49	**.001**
	Fear trial*orphaned vs. Blank trial*mother-reared	2.88	1.42, 4.34	**< .001**
	Fear trial*mother-reared vs. Fear trial*orphaned	2.01	0.28, 3.74	**.023**
Tucked tail (2 interactions: trial*mother-reared AND trial*sex)	Blank trial*mother-reared vs. Blank trial*orphaned	0.01	-0.90, 0.92	.979
	Fear trial*mother-reared vs. Blank trial*orphaned	4.26	2.78, 5.74	**< .001**
	Fear trial*mother-reared vs. Blank trial*mother-reared	4.25	2.76, 5.74	**< .001**
	Fear trial*orphaned vs. Blank trial*orphaned	1.76	0.51, 3.01	**.006**
	Fear trial*orphaned vs. Blank trial*mother-reared	1.75	0.41, 3.10	**.011**
	Fear trial*mother-reared vs. Fear trial*orphaned	2.50	1.09, 3.91	**.001**
	Blank trial*male vs. Blank trial*female	-0.50	-1.36, 0.35	.250
	Fear trial*male vs. Blank trial*male	-0.08	-1.50, 1.34	.908
	Fear trial*female vs. Blank trial*female	1.76	0.51, 3.01	**.006**
	Fear trial*female vs. Blank trial*male	2.27	0.98, 3.55	**.001**
	Fear trial*male vs. Blank trial*female	-0.59	-2.00, 0.82	.414
	Fear trial*male vs. Fear trial*female	-2.35	-3.73, -0.97	**.001**

Table 2c

Results from Mixed Poisson or Negative Binomial Regression Models for Responses of Kittens During 10-sec Stimulus Presentations (i.e., Immediate Responses) During Fear Trials When Kittens Avoided a Stimulus (n = 68) Compared to Blank Trials (referent; n = 175)[a]

Behavior	Variable(s) or interaction term(s)	Incidence rate ratio (IRR)	95% CI	P-value
Ears back[NB]	Blank trial	REFERENT		
	Fear trial	3.29	2.26, 4.81	**< .001**
Flinching[P]	Blank trial	REFERENT		
	Fear trial	18.01	5.37, 60.39	**< .001**
Paw lifting[NB]	Blank trial	REFERENT		
	Fear trial	1.15	0.54, 2.45	.711
Lip licking[NB]	Blank trial	REFERENT		
	Fear trial	0.85	0.32, 2.27	.744
Meowing[NB]	Blank trial	REFERENT		
	Fear trial	0.13	0.11, 1.45	.097
Growling[P]	Blank trial	REFERENT		
	Fear trial	$6.89*10^{7}$	0.00, ∞	.996
Hissing[P]	Blank trial	REFERENT		
	Fear trial	Model did not converge		

Note. [P]Poisson regression model; [NB]Negative binomial regression model. [a] Variance components from each mixed model: Ears back: litter level = 0.04 (95% Confidence Interval: $5.84*10^{-4}$, 2.52); kitten level = 0.05 ($5.91*10^{-4}$, 4.61); Flinching: litter level = $6.45*10^{-35}$ (NA, NA); kitten level = $3.33*10^{-33}$ (NA, NA); Paw lifting: litter level = 0.20 (0.02, 1.71); kitten level = $6.28*10^{-34}$ (NA, NA); Lip licking: litter level = $1.13*10^{-34}$ (NA, NA); kitten level = $3.12*10^{-33}$ (NA, NA); Meowing: litter level = 7.63 (1.08, 53.79); kitten level = $6.32*10^{-37}$ (NA, NA); Growling: litter level = $3.67*10^{-33}$ (NA, NA); kitten level = $1.91*10^{-30}$ (NA, NA); Hissing: NA.

Table 3a

Results From Mixed Linear Regression Models for Responses of Kittens During 30 s Behavior Observation Periods After Stimulus Removal (i.e., Delayed Responses) During Fear Trials When Kittens Avoided a Stimulus (n = 68) Compared to Blank Trials (Referent; n = 177), Including Random Intercepts for Litter and Kitten [a]

Behavior (sec)	Variable(s) or Interaction term(s)	β	95% CI	P-value
Arched back[b] (interaction: trial*coat color)	Blank trial	REFERENT		
	Fear trial	0.16	-0.75, 1.07	.737
	Black coat color	REFERENT		
	Gray coat color	0.05	-0.81, 0.90	.917
	White coat color	0.08	-0.89, 1.04	.879
	Tabby coat color	0.06	-0.73, 0.86	.874
	Tri-color coat color	0.05	-0.98, 1.07	.930
	Blank trial*black coat color	REFERENT		
	Fear trial*gray coat color	-0.15	-1.72, 1.42	.851
	Fear trial*white coat color	3.54	1.88, 5.21	**< .001**
	Fear trial*tabby coat color	-0.16	-1.54, 1.21	.818
	Fear trial*tri-color coat color	-0.13	-2.19, 1.92	.898
Crouching	Blank trial	REFERENT		
	Fear trial	1.70	0.30, 3.10	**.018**
	Black coat color	REFERENT		
	Gray coat color	1.32	-1.08, 3.71	.280
	White coat color	-0.55	-3.01, 1.90	.660
	Tabby coat color	-0.12	-2.32, 2. 80	.915
	Tri-color coat color	4.05	1.29, 6.81	**.004**
Piloerection[b] (interaction: trial*coat color)	Blank trial	REFERENT		
	Fear trial	3.32	0.62, 6.02	**.016**
	Black coat color	REFERENT		
	Gray coat color	0.45	-2.30, 3.21	.748
	White coat color	-1.25	-4.29, 1.80	.422
	Tabby coat color	-0.86	-3.40, 1.68	.507
	Tri-color coat color	-0.61	-3.85, 2.64	.714
	Blank trial*black coat color	REFERENT		
	Fear trial*gray coat color	2.30	-2.35, 6.96	.333
	Fear trial*white coat color	4.28	-0.66, 9.23	.089
	Fear trial*tabby coat color	-0.88	-4.97, 3.21	.673
	Fear trial*tri-color coat color	7.87	1.76, 13.98	**.012**
Freezing	Blank trial	REFERENT		
	Fear trial	8.39	6.48, 10.29	**< .001**
Slow walking	Blank trial	REFERENT		
	Fear trial	1.32	-0.40, 3.04	.132
In hutch	Blank trial	REFERENT		
	Fear trial	-1.35	-3.14, 0.44	.140
Tucked tail[b] (interaction: trial*mother-reared)	Blank trial	REFERENT		
	Fear trial	2.84	0.56, 5.11	**.015**
	Orphaned	REFERENT		
	Mother-reared	0.19	-1.68, 2.06	.841
	Blank trial*orphaned	REFERENT		
	Fear trial*mother-reared	3.96	0.52, 7.41	**.024**
Upright tail	Blank trial	REFERENT		
	Fear trial	-1.94	-3.35, -0.52	**.007**
	Black coat color	REFERENT		
	Gray coat color	-3.75	-6.06, -1.45	**.001**
	White coat color	-2.49	-5.06, 0.07	.057
	Tabby coat color	-3.73	-5.84, -1.62	**.001**
	Tri-color coat color	-4.03	-6.85, -1.21	**.005**
Tail lash	Blank trial	REFERENT		
	Fear trial	-0.01	-0.02, 0.01	.532
Eating	Blank trial	REFERENT		
	Fear trial	-5.56	-8.22, -2.91	**< .001**

Note. [a] Variance components from each mixed model: Arched back: litter level = 0.05 (95% Confidence Interval: 0.00, 22.33), kitten level = 0.03 ($1.31*10^{-8}$, 61475.74), observation level = 3.53 (2.89, 4.31); Crouching: litter level = 2.62 (0.67, 10.23); kitten level = 0.23 ($2.37*10^{-6}$, $2.14*10^{4}$); observation level = 24.32 (19.98, 29.61); Piloerection: litter level = 1.26 (0.10, 16.00); kitten level = 0.57 ($1.37*10^{-3}$, 239.89); observation level = 30.94 (25.41, 36.68); Freezing: litter level = 1.52 (0.12, 19.70); kitten level = 0.49 ($2.66*10^{-5}$, $8.99*10^{3}$); observation level = 45.80 (37.68, 55.66); Slow walking: litter level = 2.05 (0.40, 10.59); kitten level = $6.82*10^{-12}$ ($1.86*10^{-17}$, $2.50*10^{-6}$); observation level = 37.31 (31.06, 44.82); In hutch: litter level = 2.12 (0.39, 11.54); kitten level = 1.06 (0.02, 53.81); observation level = 40.11 (32.96, 48.83); Tucked tail: litter level = 0.11 ($8.78*10^{-9}$, $1.40*10^{6}$); kitten level = $1.96*10^{-10}$ ($5.37*10^{-16}$, $7.16*10^{-5}$); observation level = 37.19 (30.94, 44.69); Upright tail: litter level = 0.26 ($1.11*10^{-5}$, $5.94*10^{3}$); kitten level = 2.27 (0.48, 10.70); observation level = 24.76 (20.36, 30.11); Tail lash: litter level = 6.13*10-11 (95% Confidence Interval: 1.54*10-21, 2.45), kitten level = 8.23*10-14 (0.00, ∞), observation level = 0.004 (0.003, 0.005); Eating: litter level = 13.96 (4.75, 40.99); kitten level = $2.88*10^{-11}$ ($6.40*10^{-17}$, $1.29*10^{-5}$); observation level = 88.29 (73.52, 106.03). [b] Please see Table 3b for the interpretation effects of the interactions.

Table 3b

Contrasts of Selected Combinations of Interacting Variables From Mixed Linear Regression Models Presented in Table 3a

Behavior (sec)	Interaction comparisons	β	95% CI	P-value
Arched back (interaction: trial*coat color)	Fear trial*gray coat vs. Blank trial*gray coat	0.01	-1.27, 1.28	.993
	Fear trial*black coat vs. Blank trial*black coat	0.16	-0.75, 1.07	.737
	Fear trial*white coat vs. Blank trial*white coat	3.70	2.30, 5.09	< .001
	Fear trial*tabby coat vs. Blank trial*tabby coat	-0.01	-1.04, 1.03	.992
	Fear trial*tri-color coat vs. Blank trial*tri-color coat	0.02	-1.82, 1.87	.982
	Fear trial*gray coat vs. Fear trial*black coat	-0.11	-1.48, 1.27	.881
	Fear trial*gray coat vs. Fear trial*white coat	-3.72	-5.37, -2.08	< .001
	Fear trial*gray coat vs. Fear trial*tabby coat	-0.01	-1.46, 1.44	.991
	Fear trial*gray coat vs. Fear trial*tri-color coat	-0.02	-2.05, 2.01	.987
	Fear trial*black coat vs. Fear trial*white coat	-3.62	-5.04, -2.20	< .001
	Fear trial*black coat vs. Fear trial*tabby coat	0.10	-1.09, 1.29	.873
	Fear trial*black coat vs. Fear trial*tri-color coat	0.09	-1.76, 1.93	.925
	Fear trial*white coat vs. Fear trial*tabby coat	3.71	2.22, 5.20	< .001
	Fear trial*white coat vs. Fear trial*tri-color coat	3.71	1.65, 5.76	< .001
	Fear trial*tabby coat vs. Fear trial*tri-color coat	-0.01	-1.91, 1.89	.993
Piloerection (interaction: trial*coat color)	Fear trial*gray coat vs. Blank trial*gray coat	5.62	1.83, 9.42	.004
	Fear trial*black coat vs. Blank trial*black coat	3.32	0.62, 6.02	.016
	Fear trial*white coat vs. Blank trial*white coat	7.61	3.47, 11.74	< .001
	Fear trial*tabby coat vs. Blank trial*tabby coat	2.44	-0.64, 5.52	.120
	Fear trial*tri-color coat vs. Blank trial*tri-color coat	11.19	5.71, 16.67	< .001
	Fear trial*gray coat vs. Fear trial*black coat	2.75	-1.46, 6.96	.200
	Fear trial*gray coat vs. Fear trial*white coat	-0.29	-5.33, 4.76	.912
	Fear trial*gray coat vs. Fear trial*tabby coat	4.50	-0.01, 9.00	.051
	Fear trial*gray coat vs. Fear trial*tri-color coat	-4.51	-10.71, 1.69	.154
	Fear trial*black coat vs. Fear trial*white coat	-3.04	-7.38, 1.30	.170
	Fear trial*black coat vs. Fear trial*tabby coat	1.74	-1.95, 5.44	.352
	Fear trial*black coat vs. Fear trial*tri-color coat	-7.26	-12.87, -1.66	.011
	Fear trial*white coat vs. Fear trial*tabby coat	4.78	0.21, 9.35	.040
	Fear trial*white coat vs. Fear trial*tri-color coat	-4.22	-10.44, 2.00	.183
	Fear trial*tabby coat vs. Fear trial*tri-color coat	-9.01	-14.79, -3.22	.002
Tucked tail (interaction: trial*mother-reared)	Blank trial*mother-reared vs. Blank trial*orphaned	0.19	-1.68, 2.06	.841
	Fear trial*mother-reared vs. Blank trial*orphaned	6.99	4.47, 9.51	< .001
	Fear trial*mother-reared vs. Blank trial*mother-reared	6.80	4.21, 9.39	< .001
	Fear trial*orphaned vs. Blank trial*orphaned	2.84	0.56, 5.11	.015
	Fear trial*orphaned vs. Blank trial*mother-reared	2.65	0.23, 5.06	.032
	Fear trial*mother-reared vs. Fear trial*orphaned	4.15	1.21, 7.10	.006

Table 3c

Results From Mixed Negative Binomial Regression Models for Responses of Kittens During 30 s Behavior Observation Periods After Stimulus Removal (i.e., Delayed Responses) During Fear Trials When Kittens Avoided a Stimulus (n = 68) Compared to Blank Trials (Referent; n = 175)[a]

Behavior	Variable(s) or interaction term(s)	Incidence rate ratio (IRR)	95% CI	P-value
Ears back[NB]	Blank trial	REFERENT		
	Fear trial	2.21	1.64, 2.98	**< .001**
Flinching[P]	Blank trial	REFERENT		
	Fear trial	2.61	-0.65, 10.49	.176
Paw lifting[NB]	Blank trial	REFERENT		
	Fear trial	1.57	0.87, 2.80	.131
Lip licking[NB]	Blank trial	REFERENT		
	Fear trial	1.31	0.61, 2.82	.492
Meowing[NB]	Blank trial	REFERENT		
	Fear trial	0.20	0.03, 1.55	.124
Growling[NB]	Blank trial	REFERENT		
	Fear trial	104.41	0.54, 20301.91	.084
Hissing[P]	Blank trial	REFERENT		
	Fear trial	Model did not converge		

Note. [P]Poisson regression model; [NB]Negative binomial regression model. [a] Variance components from each mixed model: *Ears back*: litter level = 0.11 (95% Confidence Interval: 0.02, 0.52); kitten level = 0.06 ($3.47*10^{-3}$, 1.12); *Flinching*: litter level = $3.34*10^{-35}$ (NA, NA); kitten level = 0.32 ($3.67*10^{-4}$, 272.00); *Paw lifting*: litter level = 0.15 ($8.74*10^{-3}$, 2.44); kitten level = 0.33 (0.05, 2.01); *Lip licking*: litter level = 0.93 (0.29, 3.00); kitten level = 0.93 (NA, NA); *Meowing*: litter level = 6.02 (1.72, 21.10); kitten level = $7.09*10^{-34}$ (NA, NA); *Growling:* litter level: $1.85*10^{-32}$ (NA, NA); kitten level: $1.38*10^{-32}$ (NA, NA); *Hissing:* NA.

Table 4

Summary of All Behaviors Increased or Decreased in Kittens During and After Stimulus Presentation Compared Between Fear Trials When Kittens Avoided a Stimulus (n = 68) and Blank Trials (n = 175)

Behavior *increased* during fear trials both during and after stimulus presentation	Behavior *increased* during fear trials only during stimulus presentation	Behavior *increased* during fear trials only after stimulus removal
Arched back (only for female kittens during stimulus presentation; only for white kittens after stimulus removal) *Piloerection* (for all kittens during stimulus presentation; only for tri-color kittens after stimulus removal) *Freezing* (for mother-reared kittens during stimulus presentation + for gray and tri-color kittens in all trials; for all kittens after stimulus removal) *Tucked tail* (only for mother-reared kittens and female kittens during stimulus presentation; only for mother-reared kittens after stimulus removal) *Ears back*	*Flinching*	*Crouching* (+ increased for tri-color kittens in all trials)
Behavior *decreased* during fear trials both during and after stimulus presentation	**Behavior *decreased* during fear trials only during stimulus presentation**	**Behavior *decreased* during fear trials only after stimulus removal**
Eating *Upright tail* (only for gray and tabby coat colors during stimulus presentation in all trials; for all kittens after stimulus removal + for gray, tabby, and tri-color kittens after stimulus removal in all trials)	*Time in hutch*	

Assessing Carry-Over Effects Across Trials

As indicated above, predicted fear behaviors were generally significantly higher during stimulus trials compared to blank trials. No pattern, progression, or increase of response was found across trials, suggesting successive trials did not cause an increase in fear behaviors and that blank trials in between each stimulus presentation were successful at bringing kittens back to baseline. For full values, please see Tables S4a, b and S5a, b in Supplemental Material.

Variance Partition Components

The variance components for the random intercepts from each linear model (see footnotes in Tables 2a, 3a for full values) were used to calculate variance partition components (VPCs) for each behavior to determine the variance at each level of the models (i.e., litter-level, kitten-level). VPCs for the behaviors of arched back (26.5%), crouching (18.7%), and upright tail (22.6%) were notably higher at the kitten level, suggesting greater within-kitten effects than between litters.

Model Fit and Assumptions for Mixed Models

There were no issues with collinearity or violations of the linearity assumption, so no independent variables were removed, transformed, or categorized. Across all models, there were no concerning outliers based on standardized (linear regression models) and Pearson (rate regression models) residuals. Visual analysis of the best linear unbiased predictors (BLUPs) indicated constant variance and normality.

Discussion

This study aimed to determine which behaviors kittens display when they are avoiding a novel, unpredictable, and noisy stimulus based on the *a priori* assumption that kittens would avoid a novel stimulus when fearful (Adolphs, 2013; Archer, 1979). During blank trials, instances of avoidance were rare, indicating that kittens were comfortable in the testing environment without any stimuli present. In contrast, avoidance was common during and following stimulus presentations, suggesting that the stimuli and testing procedure were effective for inducing acute fear and identifying fear responses in kittens. We found that arched back, piloerection, freezing, tucked tail, and ears drawn back were associated with being fearful across both experimental time phases (i.e., during stimulus presentation and after stimulus removal), suggesting these behaviors may be more generalized fear responses with some exceptions for certain kitten characteristics (see section on interaction effects above). Flinching increased during the stimulus presentations, suggesting an immediate fearful action analogous to a startle response indicating acute fear. Time spent crouching, however, was longer only after the stimulus had been removed, suggesting a lingering fear response related to vigilance and ongoing threat assessment. Differences in physiological measures and response to anxiolytic drugs or treatment are often used in combination to distinguish between these states (e.g., Davis et al., 2010); however, these were not assessed here. We also found that durations of eating and upright tail were longer during blank trials, suggesting these behaviors are positive and occur when kittens are not fearful, again with some exceptions for certain kitten characteristics (see section on interaction effects above).

In adult cats, behaviors such as freezing (Adamec et al., 1980; Stella & Croney, 2019), piloerection (Ellis, 2018; Fraser, 2012; Johansson et al., 1979), arched back (Johansson et al., 1979), and side and back ear positions (Delgado et al., 1954; Fernandez de Molina & Hunsperger, 1959; Kaada et al., 1953; Leyhausen, 1979; Ursin & Kaada, 1960) have been found to be indicative of fear and stress. Further, piloerection and arched back behaviors in response to a threatening visual stimulus have been found to occur in both 6-week-old kittens and adult cats in the same experiment (Kolb & Nonneman, 1975). In the current study, arched back, piloerection, freezing, and ears drawn back were commonly observed and were displayed for significantly longer durations and greater rates during fear trials, confirming they are fully developed fear responses in 5-to 8-week-old kittens.

Other fear-related behaviors previously reported in adult cats were present in the current study but were not significantly different between trials or were not observed in a high enough proportion of kittens to allow for model convergence. Lip licking has been found to occur in adult cats during negative situations, including avoidance of a human, and it has been suggested that this behavior might indicate pain or anxiety (Frank, 2014; Gourkow & Phillips, 2015, 2016; Stella et al., 2014). While some kittens displayed lip licking in the current study, it was not a common response to the particular stimuli tested. Previous research has found that dogs show increased lip licking in response to negatively versus positively valenced photos, suggesting the response is related to emotional cues (Albuquerque et al., 2018). While no similar studies have been conducted with cats, it is possible that the static cat and dog models used in the current study were insufficient to elicit lip licking due to a lack of emotional valence in their facial expressions. These models also lacked olfactory cues, which can be important for particular types of social communication in cats (Vitale Shreve & Udell, 2017). Olfaction is an important aspect of early kitten behavioral development, particularly for nest orientation prior to weaning. Kittens as young as one week of age are able to distinguish between odour cues from their home cage versus odour cues from an unfamiliar queen and her litter (e.g., Freeman & Rosenblatt, 1978), suggesting that olfactory cues might have the potential to alter lip licking, as well as other kitten responses, in the cat model.

Other behaviors that were not observed in a sufficient proportion of kittens for complete analyses included tail lashing and hissing. While a small number of kittens displayed these behaviors in the current study, confirming they are present in kittens of this age range, they may be more extreme responses that were rare with the relatively mild stimuli presented. Vocalizations like hissing are a defensive response to a threat in domestic cats and tend to occur in more extreme situations of fear or stress (Amat et al., 2016) and would be expected to be more common when a threatening receiver is present (reviewed in Rendall et al., 2009). In previous research, orphaned neonate kittens produced more distress calls during nest separation compared to mother-reared kittens, suggesting vocalizations occur in response to stressful situations for this age group (Lowell et al., 2020). However, these responses may change as kittens age and the types of vocalizations expected in the current context differ in terms of meaning (i.e., care-soliciting distress calls versus defensive hisses).

Across all analyses, we did not find strong litter effects, which is not surprising given that litters were fostered through the same humane society and would have received at least somewhat similar experiences within their foster homes. Rather, the variance partition components from the multilevel models indicated a substantial amount of the variance was at the kitten level, particularly for the behaviors of arched back, crouching, and upright tail during the stimulus presentation phase, suggesting greater within-kitten effects than between litters due to individual differences in response. In previous research, individual variability has been found among vocalizations and activity levels in adult cats (Urrutia et al., 2019) and kittens (Hudson et al., 2015; Lowell et al., 2020; Raihani et al., 2014), among social behavior between male and female adult cats (Barry & Crowell-Davis, 1999), and among approach behavior and bold personality between kittens with different paternal genetic influences (McCune, 1995). Future research could investigate individual differences in kitten characteristics and personality in more detail to attempt to further disentangle the variation observed.

One individual kitten characteristic that was associated with fear responses in the current study was coat color. Kittens with black coats displayed longer durations of upright tail compared to all other coat colors, which is considered a positive and affiliative behavior (e.g., Brown and Bradshaw, 2014). In contrast, kittens with tri-color coats (i.e., calico and tortoiseshell) and gray coats displayed longer durations of freezing and crouching compared to kittens with black coats. During fear trials, coat color was also associated with the display of arched back (with white kittens displaying longer durations compared to all other coat colors), and piloerection (with white kittens displaying longer durations compared to tabby kittens, and tri-color kittens displaying longer durations compared to black and tabby kittens). Coat color has also been found to have varying associations with caretaker-reported behavior in cats. For example, tri-color cats have been perceived as having "tortitude" and as being more intolerant and aloof, according to caretaker survey reports (Delgado, Munera, and Reevy, 2012). Some additional studies have found subtle differences between coat colors (González-Ramírez & Landero-Hernández, 2022; Stelow et al., 2016), whereas other studies have not (Dantas-Divers et al., 2011). In general, the influence of coat color is thought to be associated with the effect of melanin on neurotransmitters linking pigmentation and behavior or personality (reviewed by González-Ramírez and Landero-Hernández, 2022), but behavioral differences have also been linked to breed (Wilhelmy et al., 2016). In the current study, all kittens were domestic short- or medium-haired (i.e., not purebred), as is anecdotally common in the population of kittens within shelter systems. The differences in coat color, particularly for the positive behavior of upright tail, suggest that kittens with black coats display less fearful behavior. This finding may help reduce the bias against adopting black cats (Jones & Hart, 2020), which could improve their chances of successful adoption. Another practical application could include focusing enhanced or modified socialization efforts for kittens with other coat colors, such as tri-color and white coats, who were more likely to display fear behaviors, in an effort to mitigate the display and persistence of a fearful emotional state.

In addition to coat color, we also found a number of interesting interactions with other kitten demographics and characteristics. Previous research has not found differences between male and female cats in terms of fear or stress behaviors (Hudson et al., 2015; Warren & Levy, 1979), social dominance (Durr & Smith, 1997), or behavior at feeding occasions (Bradshaw & Cook, 1996). However, we found female kittens displayed longer durations of arched back and tucked tail than male kittens during fear trials, suggesting sex has an impact on the display of these behaviors. Importantly, arched back and tucked tail were not significantly different in male kittens between fear and blank trials, suggesting these behaviors may not be indicative of fear in the male sex or that male kittens are generally less fearful. Mother-reared kittens also showed more exaggerated responses during fear trials compared to orphaned kittens, possibly because their responses were reinforced with care provision by the mother cat while those of orphaned kittens were not. Most previous research on care-soliciting behavior has been focused on vocalizations, which have been found to elicit maternal attention in many species, including cats (Bánszegi et al., 2017; Haskins, 1977) and rodents (Bell et al., 1974). However, it is likely that mothers also respond to other cues from their kittens beyond vocalizations. Alternatively, the maternal and littermate separation in the current study might have been an added stressor that increased responses in mother-reared kittens. However, the duration of separation was approximately 10 minutes and likely not long enough to induce lasting impacts, such as those observed in, for example, laboratory studies of maternal separation which can be hours, days, or even months (e.g., reviewed in Latham and Mason, 2008).

Limitations

The results of the current study may not be representative of the general kitten population. The foster caretakers who enrolled their kittens in the study may have been more interested in animal behavior and welfare and may have provided more socialization experiences than the average kitten foster or caretaker, potentially resulting in selection bias. As this research was conducted within foster caretakers' homes, there was large variation in the characteristics of what those environments looked like, particularly in terms of exposure to other animals (ranging from none to many, e.g., other cats, dogs, chickens), exposure to humans (ranging from one human caretaker in the household to large families with children), and size of the available space (ranging from one bathroom or bedroom in an apartment to full access to a multi-room, multi-story house). Detailed household demographic information, such as previous exposure to dogs, would be useful for future research to compare responses between characteristics. While the behavior assessment used in the current study was successful at eliciting fear behavior in this population of participating kittens, it is possible that less socialized kittens may have displayed more exaggerated or different fear responses which may have influenced the range of behaviors identified and analyzed. Variation in environmental characteristics may also have influenced the differences observed in the proportion of kittens displaying avoidance to each stimulus. If kittens with fewer socialization experiences displayed more extreme responses due to lack of previous exposure, we may have expected less frequently occurring behaviors (e.g., tail lashing, hissing) to have become more common; however, we do not expect the responses themselves to be fundamentally different than those occurring in less socialized kittens. While the behaviors observed in the current study reflected responses within a fear context, it is also possible that these behaviors are present in other situations involving negative affect, such as pain, and would require further testing in different contexts. It is also possible that kittens display unique behaviors compared to adult cats, which were used to create the ethogram for the current study, and additional age-specific behaviors should be considered in future research.

Kittens in the current study were separated from their littermates and mother (if she was present) during testing, and this separation might have resulted in an increased level of baseline stress, particularly for mother-reared kittens. However, we would have expected similar responses during both blank and stimulus trials, and we found clear differences between trials suggesting separation was not a major factor. We also did not investigate differences in age within the current study as kitten age was estimated from shelter intake information and it was therefore uncertain how accurate these estimates were, given that many kittens came in as strays. Kittens in the current study were estimated to be between 5 and 8 weeks of age based on crude developmental timepoints, so we are confident in the general range but not the specific ages of the individuals. If this information were available for future studies, it could be possible to distinguish between subtle differences in the behavioral development of kittens within their socialization period.

Conclusions

The behavior assessment used in the current study involved exposure to novel social and non-social stimuli representing "everyday" experiences and was successful at eliciting fear responses in 5-to-8-week-old kittens. Fear behaviors observed in these kittens included arched back, crouching, piloerection, freezing, tucked tail, ears drawn back, and flinching, with kitten characteristics impacting the effect of some behaviors. Neutral and positive behaviors observed—that is, those displayed for longer durations during blank control trials—included eating and upright tail. We did not see any increase in fear response over the course of the behavior assessment, therefore the model used in this study was appropriate for our objective. Thus, our findings confirm a similar behavioral repertoire in young kittens as is observed in adult cats. Nevertheless, individual responses varied with kitten characteristics and further research would benefit from a wider range of stimulus exposures, individual kitten personality assessments, and/or testing in standardized laboratory-like environments.

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Supplementary Material

Table S1

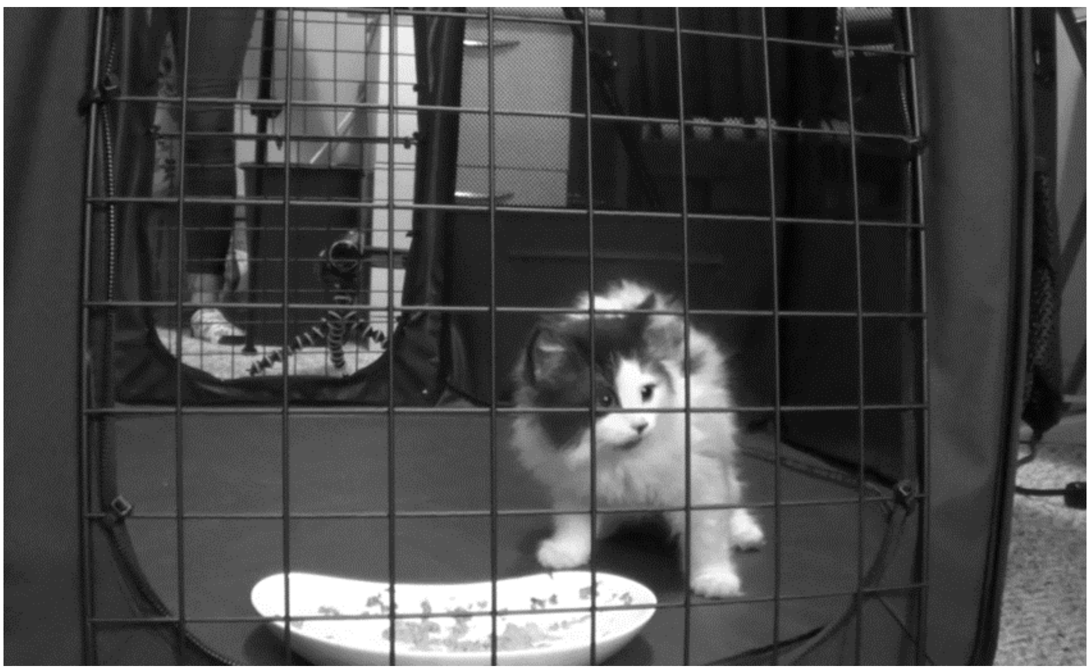
Audio Clips of Stimulus Presentations for Behavior Test Assessing Fear in Kittens in Response to Novel Social and Non-Social Stimuli

Stimulus	Link
Cat	https://www.youtube.com/watch?v=jePP2BYj8ag
Dog	https://www.youtube.com/watch?v=5mW045eetSk
Vacuum	https://www.youtube.com/watch?v=TI-6Cl9Ndqg

Figure S1a.

Note. Still from a video example of a blank control trial during a behavior test assessing kitten fear responses to two different novel social stimuli and one non-social stimulus. No stimulus was presented during this blank trial. https://youtu.be/Mcvm4HMvhmE

Figure S1b.



Note. Still from a video example of a stimulus trial (dog) during a behavior test assessing kitten fear responses to two different novel social stimuli and one non-social stimulus. This kitten displayed avoidance—the *a priori* criterion indicating fear—therefore this trial was classified as "fearful". https://youtu.be/QQ-1iaFcAPc *(Immediate noise warning—dog barking)*

Table S2

Descriptive Statistics for Kittens (n = 46) Who Completed a Behavioral Test Assessing Fear Responses to Two Different Novel Social Stimuli and One Non-Social Stimulus

Litter ID	Kitten Name	Sex	Coat color[a]	Est. Age (weeks)	With mom in foster care	Number of avoid trials[b]
9	Althea	Female	Gray	5	No	0
9	Artemis	Male	Gray	5	No	0
9	Diana	Female	Black	5	No	1
9	Mala	Female	Gray	5	No	1
9	Nibia	Female	Gray	5	No	2
11	Lou	Male	Black	5	Yes	2
11	Milo	Female	Tri-color	5	Yes	0
11	Nova	Male	Black	5	Yes	1
11	Remi	Female	Tri-color	5	Yes	1
11	Tilly	Female	Tri-color	5	Yes	1
3	Eeny	Male	Gray	6	Yes	2
3	Meeny	Male	Gray	6	Yes	1
3	Miny	Male	Gray	6	Yes	1
13	Brie	Female	Tabby	6.5	No	2
13	Parm	Female	Tabby	6.5	No	3
1	Apollo	Male	Tabby	7	Yes	3
1	Gaia	Female	Tabby	7	Yes	2
1	Hera	Female	Tabby	7	Yes	1
1	Jupiter	Male	Tabby	7	Yes	1
1	Orion	Male	Tabby	7	Yes	1
2	Penelope	Female	Black	7	No	3
2	Rose	Female	Black	7	No	2
4	Dusty	Female	White	7	No	1
4	Magic	Female	Black	7	No	1
4	Pepper	Male	Black	7	No	2
5	Dottie	Female	Tri-color	7	Yes	1
5	Evelyn	Female	White	7	Yes	2
5	Jimmy	Male	Tabby	7	Yes	3
5	Kit	Female	Tri-color	7	Yes	2
10	Alley	Female	White	7	No	1
10	Leonard	Male	Black	7	No	1
10	Lowry	Male	Tabby	7	No	1
10	Spalding	Male	White	7	No	2
10	Swish	Female	White	7	No	2
12	Griffin	Male	Gray	7	No	2
12	Kitty Queen	Female	Black	7	No	3
6	Joe	Male	White	7.5	No	2
6	Kevin	Male	Tabby	7.5	No	0
6	Nick	Male	Gray	7.5	No	2
7	Brick	Male	Black	7.5	Yes	0
7	Cinder	Female	Black	7.5	Yes	3
7	Kohl	Male	Black	7.5	Yes	2
8	Moon	Male	Black	8	No	2
8	Owl	Female	Tabby	8	No	1
8	Sun	Male	Black	8	No	1
8	Train	Male	Tabby	8	No	0

Note. [a] Coat color was determined by the experimenter and recorded as the majority color of the kitten's fur (e.g., if a kitten was mostly black with white paws and/or a white tuft, coat color was marked as "black"), "white" included all white, and mostly white (e.g., primarily white with black or gray); "tri-color" included calico and tortoiseshell; and "tabby" included gray, brown, and orange tabby. [b] Highest possible number of "avoid" trials (i.e., stimulus trials in which the kitten showed avoidance) is 3.

Table S3

Number and Proportion of Total Kittens (n = 46) Performing Each Behavior At Least Once Across All Trials During a Behavioral Test Assessing Kitten Fear Responses to Two Different Novel Social Stimuli and One Non-Social Stimulus

Behavior	Variable type	# of kittens showing behavior	Proportion of total kittens
Arched back	Duration	11	0.24
Crouching	Duration	28	0.61
Piloerection	Duration	16	0.35
Freezing	Duration	41	0.89
Slow walking	Duration	36	0.78
In hutch	Duration	24	0.52
Tail upright	Duration	19	0.41
Tail tucked	Duration	21	0.46
Eating	Duration	31	0.67
Lip lick	Count	38	0.83
Flinch	Count	22	0.48
Paw lift	Count	37	0.80
Ears back	Count	45	0.98
Tail lash*	Count	1	0.02*
Growl*	Count	3	0.07*
Hiss*	Count	6	0.13*
Meow	Count	17	0.37

Note. *Behaviors occurring in less than 25% of kittens were not used for regression analyses.

Table S4a

Results From Mixed Linear Regression Models for Responses of Kittens During 10 Sec Stimulus Presentations (i.e., Immediate Responses) During Fear Trials When Kittens Avoided a Stimulus (N = 68) Compared to Blank Trials (Referent; N = 175) By Trial Code.

Behavior (sec)	Trial code	β	95% CI	P-value
Crouching	1st control trial	REFERENT		
	1st stimulus trial	0.50	-0.36, 1.36	.256
	2nd control trial	0.66	-0.06, 1.38	.074
	2nd stimulus trial	0.80	-0.13, 1.72	.092
	3rd control trial	0.65	-0.08, 1.39	.080
	3rd stimulus trial	-0.04	-0.97, 0.89	.934
	4th control trial	0.80	0.05, 1.55	**.036**
Piloerection	1st control trial	REFERENT		
	1st stimulus trial	1.90	0.44, 3.36	**.011**
	2nd control trial	-0.02	-1.28, 1.22	.975
	2nd stimulus trial	1.80	0.23, 3.37	**.024**
	3rd control trial	0.21	-1.04, 1.46	.742
	3rd stimulus trial	3.62	2.06, 5.18	**< .001**
	4th control trial	0.44	-0.84, 1.71	.501
Freezing	1st control trial	REFERENT		
	1st stimulus trial	2.61	0.85 4.36	**.004**
	2nd control trial	-0.08	-1.58, 1.42	.916
	2nd stimulus trial	3.77	1. 88, 5.65	**< .001**
	3rd control trial	0.11	-1.40, 1.63	.886
	3rd stimulus trial	3.99	2.11, 5.878	**< .001**
	4th control trial	0.74	-0.80, 2.28	.349
Slow walking	1st control trial	REFERENT		
	1st stimulus trial	0.10	-0.62, 0.81	.793
	2nd control trial	0.38	-0.23, 0.98	.226
	2nd stimulus trial	0.11	-0.65, 0.88	.773
	3rd control trial	0.34	-0.27, 0.95	.275
	3rd stimulus trial	0.22	-0.55, 0.98	.578
	4th control trial	1.00	0.37, 1.62	**.002**
In hutch	1st control trial	REFERENT		
	1st stimulus trial	-0.23	-1.09, 0.63	.604
	2nd control trial	0.52	-0.21, 1.25	.164
	2nd stimulus trial	0.07	-0.85, 0.99	.870
	3rd control trial	1.10	0.36 1.84	**.003**
	3rd stimulus trial	-0.23	-1.15, 0.69	.629
	4th control trial	0.19	-0.56, 0.95	.615
Tucked tail	1st control trial	REFERENT		
	1st stimulus trial	1.62	0.21, 3.03	**.025**
	2nd control trial	0.01	-1.19, 1.20	.994
	2nd stimulus trial	2.76	1.25, 4.27	**< .001**
	3rd control trial	0.82	-0.39, 2.03	.183
	3rd stimulus trial	2.59	1.08, 4.01	**.001**
	4th control trial	0.20	-1.03, 1.43	.751
Upright tail	1st control trial	REFERENT		
	1st stimulus trial	0.46	-0.38, 1.29	.283
	2nd control trial	0.55	-0.14, 1.25	.119
	2nd stimulus trial	0.68	-0.22, 1.57	.139
	3rd control trial	0.79	0.09, 1.50	**.027**
	3rd stimulus trial	0.10	-0.80, 0.99	.835
	4th control trial	0.28	-0.44, 0.99	.453
Eating	1st control trial	REFERENT		
	1st stimulus trial	-4.86	-6.07, -3.66	**< .001**
	2nd control trial	-3.57	-4.58, -2.55	**< .001**
	2nd stimulus trial	-5.22	-6.51, -3.92	**< .001**
	3rd control trial	-4.72	-5.74, -3.69	**< .001**

3rd stimulus trial	-5.12	-6.97, -3.91	**< .001**
4th control trial	-4.62	-5.66, -3.57	**< .001**

Table S4b

Results From Mixed Poisson And Negative Binomial Regression Models For Responses Of Kittens During 10 Sec Stimulus Presentations (i.e., Immediate Responses) During Fear Trials When Kittens Avoided A Stimulus (N = 68) Compared To Blank Trials (Referent; N = 175) By Trial Code.

Behavior	Stimulus type	Incidence rate ratio (IRR)	95% CI	P-value
Ears back[NB]	1st control trial	REFERENT		
	1st stimulus trial	4.55	2.51, 8.26	**< .001**
	2nd control trial	0.89	0.44, 1.78	.737
	2nd stimulus trial	2.26	1.11, 4.57	**.024**
	3rd control trial	1.17	0.58, 2.35	.656
	3rd stimulus trial	3.01	1.46, 6.19	**.003**
	4th control trial	1.17	0.59, 2.30	.650
Flinching[P]	1st control trial	REFERENT		
	1st stimulus trial	13.54	1.69, 108.24	**.014**
	2nd control trial[Ex,a]	0.96	0, 600.30	.978
	2nd stimulus trial	14.67	1.80, 119.21	**.012**
	3rd control trial	1.00	0.06, 15.99	1.000
	3rd stimulus trial	12.57	1.51, 104.42	**.019**
	4th control trial	1.07	0.07, 17.16	.960
Paw lifting[NB]	1st control trial	REFERENT		
	1st stimulus trial	1.57	0.51, 4.80	.428
	2nd control trial	0.76	0.26, 2.18	.610
	2nd stimulus trial	0.42	0.08, 2.23	.314
	3rd control trial	0.51	0.16, 1.68	.271
	3rd stimulus trial	0.65	0.15, 2.73	.554
	4th control trial	0.89	0.31, 2.59	.838
Lip licking[NB]	1st control trial	REFERENT		
	1st stimulus trial	0.16	0.22, 3.84	.904
	2nd control trial	0.427	0.11, 1.73	.237
	2nd stimulus trial	0.708	0.16, 3.23	.655
	3rd control trial	0.868	0.24, 3.08	.827
	3rd stimulus trial[a]	$5.31e^{-09}$	NA	.998
	4th control trial	0.246	0.04, 1.39	.113
Meowing[NB, b]	1st control trial	REFERENT		
	1st stimulus trial	$2.08e^{+09}$	NA	.999
	2nd control trial	$9.95e^{+09}$	NA	.999
	2nd stimulus trial	$3.87e^{+08}$	NA	.999
	3rd control trial	$6.73e^{+09}$	NA	.999
	3rd stimulus trial	0.202	NA	1.000
	4th control trial	$5.99e^{+09}$	NA	.999

Note. [P]Poisson regression; [NB]Negative binomial regression; [EX]Exact Poisson regression. [a] Due to a small number of observations, an exact Poisson regression model was used without random intercepts giving median unbiased estimates where possible, and some parameters could not be estimated. b Values could not be estimated using an exact Poisson regression model.

Table S5a

Results From Mixed Linear Regression Models For Responses Of Kittens During 30 Sec Behavior Observation Periods After Stimulus Removal (i.e., Delayed Responses) During Fear Trials When Kittens Avoided A Stimulus (N = 68) Compared To Blank Trials (Referent; N = 175) By Trial Code

Behavior (sec)	Trial code	β	95% CI	P-value
Crouching	1st control trial	REFERENT		
	1st stimulus trial	1.604	-0.76, 3.97	.184
	2nd control trial	1.222	-0.78, 3.22	.231
	2nd stimulus trial	3.476	0.93, 6.02	**.007**
	3rd control trial	1.731	-0.27, 3.73	.090
	3rd stimulus trial	3.457	0.92, 5.99	**.008**
	4th control trial	1.858	-0.21, 3.92	.078
Piloerection	1st control trial	REFERENT		
	1st stimulus trial	5.335	2.60, 8.07	**< .001**
	2nd control trial	-0.044	-2.37, 2.28	.970
	2nd stimulus trial	3.515	0.57, 6.46	**.019**
	3rd control trial	0.630	-1.69, 2.95	.595
	3rd stimulus trial	6.266	3.33, 9.20	**< .001**
	4th control trial	0.741	-1.66, 3.14	.545
Freezing	1st control trial	REFERENT		
	1st stimulus trial	9.757	6.57, 12.94	**< .001**
	2nd control trial	-0.866	-3.58, 1.84	.531
	2nd stimulus trial	5.261	1.84, 8.68	**.003**
	3rd control trial	-0.219	-2.93, 2.49	.874
	3rd stimulus trial	10.644	7.23, 14.06	**< .001**
	4th control trial	2.228	-0.56, 5.08	.110
Slow walking	1st control trial	REFERENT		
	1st stimulus trial	2.632	-0.31, 5.57	.080
	2nd control trial	1.997	-0.51, 4.50	.118
	2nd stimulus trial	2.887	-0.28, 6.05	.074
	3rd control trial	1.768	-0.74, 4.27	.167
	3rd stimulus trial	2.000	-1.16, 5.14	.216
	4th control trial	0.958	-1.63, 3.54	.468
In hutch	1st control trial	REFERENT		
	1st stimulus trial	-0.070	-3.09, 2.95	.964
	2nd control trial	2.079	-0.48, 4.65	.111
	2nd stimulus trial	0.930	-2.32, 4.18	.575
	3rd control trial	3.608	1.04, 6.17	**.006**
	3rd stimulus trial	0.888	-2.35, 4.13	.591
	4th control trial	1.836	-0.81, 4.38	.174
Tucked tail	1st control trial	REFERENT		
	1st stimulus trial	6.735	3.79, 9.68	**< .001**
	2nd control trial	0.139	-2.38, 2.65	.914
	2nd stimulus trial	3.856	0.79, 7.02	**.017**
	3rd control trial	0.789	-1.73, 3.30	.538
	3rd stimulus trial	4.788	1.63, 7.94	**.003**
	4th control trial	1.897	-0.70, 4.49	.151
Upright tail	1st control trial	REFERENT		
	1st stimulus trial	-0.217	-2.62, 2.18	.860
	2nd control trial	1.3354	-0.67, 3.38	.190
	2nd stimulus trial	-0.796	-3.38, 1.79	.547
	3rd control trial	2.492	0.46, 4.52	**.016**
	3rd stimulus trial	-0.463	-3.04, 2.12	.725
	4th control trial	1.660	-0.44, 3.76	.121
Eating	1st control trial	REFERENT		
	1st stimulus trial	-12.903	-16.72, -9.09	**< .001**
	2nd control trial	-9.324	-12.55, -6.10	**< .001**
	2nd stimulus trial	-15.876	-19.98, -11.77	**< .001**
	3rd control trial	-13.637	-16.86, -10.41	**< .001**
	3rd stimulus trial	-15.525	-19.61, -11.44	**< .001**
	4th control trial	-13.888	-17.22, -10.56	**< .001**

Table S5b

Results From Mixed Poisson And Negative Binomial Regression Models For Responses Of Kittens During 30 Sec Behavior Observation Periods After Stimulus Removal (i.e., Delayed Responses) During Fear Trials When Kittens Avoided A Stimulus (N = 68) Compared To Blank Trials (Referent; N = 175) By Trial Code

Behavior	Stimulus type	Incidence rate ratio (IRR)	95% CI	P-value
Ears back[NB]	1st control trial	REFERENT		
	1st stimulus trial	3.517	2.11, 5.86	**< .001**
	2nd control trial	1.414	0.84, 2.38	.192
	2nd stimulus trial	2.445	1.35, 4.43	**.003**
	3rd control trial	1.526	0.90, 2.59	.117
	3rd stimulus trial	3.355	1.91, 5.91	**< .001**
	4th control trial	1.973	1.17, 3.33	**.011**
Flinching[EX, a]	1st control trial	REFERENT		
	1st stimulus trial	4.18	0.33, ∞	.268
	2nd control trial	1.00	0.023, ∞	1.000
	2nd stimulus trial	2.14	0.05, ∞	.636
	3rd control trial	1.00	0.03, ∞	1.000
	3rd stimulus trial	2.14	0.05, ∞	.636
	4th control trial	2.72	0.21, ∞	.443
Paw lifting[NB]	1st control trial	REFERENT		
	1st stimulus trial	1.63	0.60, 4.41	.337
	2nd control trial	1.10	0.48, 2.57	.817
	2nd stimulus trial	2.01	0.74, 5.41	.169
	3rd control trial	1.19	0.51, 2.75	.692
	3rd stimulus trial	0.80	0.26, 2.47	.700
	4th control trial	0.51	0.19, 1.38	.186
Lip licking[NB]	1st control trial	REFERENT		
	1st stimulus trial	0.96	0.26, 3.56	.955
	2nd control trial	0.76	0.25, 2.31	.632
	2nd stimulus trial	2.09	0.52, 8.39	.299
	3rd control trial	0.82	0.25, 2.73	.749
	3rd stimulus trial	0.29	0.04, 1.85	.189
	4th control trial	0.53	0.16, 1.80	.310
Meowing[NB]	1st control trial	REFERENT		
	1st stimulus trial	0.25	0.00, 6.23	.395
	2nd control trial	0.99	0.06, 17.39	.994
	2nd stimulus trial	7.02	0.26, 186.68	.224
	3rd control trial	12.01	0.90, 160.41	.060
	3rd stimulus trial	0.75	0.03, 20.81	.863
	4th control trial	3.79	0.30, 48.78	.306

Note. [NB]Negative binomial regression; [EX]Exact Poisson regression. [a] Due to a small number of observations, an exact Poisson regression model was used without random intercepts giving median unbiased estimates where possible, and some parameters could not be estimated.