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Early life adversity in dogs produces altered physiological and behavioral responses during a social stress-buffering paradigm

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Abstract

Although owners can act as stress buffers for their dogs, whether dogs with poor early life histories with humans will respond similarly is unknown. We tested 45 dogs, 23 of which were rescued from adverse conditions, in a social paradigm in which a threatening stranger confronted them with either their owner or an unfamiliar human present. Salivary cortisol levels were assessed at three points, and the dogs' behavior and owners' responses to questionnaires were evaluated. Dogs from adverse backgrounds engaged in greater contact and exhibited more relaxed behaviors and social referencing when their owners were present. Dogs from the comparison group explored more when accompanied by their owners. Dogs from adverse backgrounds experienced greater decreases in cortisol levels from the first to third samples relative to dogs in the comparison group. Dogs from adverse backgrounds were also more likely to respond fearfully to a threatening stranger. Their owners rated them as having higher levels of stranger-directed fear, nonsocial fear, separation-related problems, attention seeking, and lower levels of chasing and trainability. These findings from this study suggest that early adverse environments may have lasting effects on dogs' social behavior.

KEYWORDS
attachment, cortisol, early life history, human–animal interactions, social referencing

Attachment is a type of social bond that exists not only between offspring and their parents but in other relationships as well (Ainsworth & Bell, 1970; Higley et al., 1992; Remage-Healey et al., 2003). Attachment behavior is often defined as an individual engaging in behaviors to maintain contact and proximity with an attachment figure and exhibiting stress upon separation (Ainsworth, 1969; Bowlby, 1958, 1969; Klagsbrun & Bowlby, 1976). Originating from ethological principles, Bowlby (1969) described the construct of attachment as a regulatory system in which innate behavioral mechanisms are activated in response to specific social stimuli, thereby reducing the risk of harm from predation and enhancing safety and security (Nagasawa et al., 2009). The attachment system is activated upon separation, leading to behavioral changes to restore proximity to the attachment figure (Bowlby, 1969). Across mammalian species, even brief separation of attached individuals has been shown to evoke a response from the hypothalamic–pituitary–adrenal (HPA) axis, the neuroendocrine system that aids in stress regulation by producing cortisol, a steroid hormone secreted from the adrenal glands (Coe et al., 1978; Gunnar et al., 1981; Hennessy, 1986; Mineka & Suomi, 1978; Smotherman et al., 1979). The presence of an attachment figure acts as a "secure base" for exploration in a novel environment and provides a buffering effect on the HPA axis during stressful situations (Ainsworth, 1979, 1989; Gunnar & Donzella, 2002; Nachmias et al., 1996; Levine, 1993, Parker et al., 2006; Stanton & Levine, 1990). Thus, an individual's stress response in the presence or absence of an attachment figure provides information about the strength and quality of that attachment bond.

Attachment bonds exist within and between species (Lorenz, 1937), as exemplified by the human–dog bond (Topál et al., 1998). As a result of more than 30,000 years of domestication (Frantz et al., 2016; Freedman et al., 2014;

Larson et al., 2012; Thalmann et al., 2013; Wang et al., 2016), dogs are attuned to the communicative and emotional states of humans, allowing them to engage in complex social interactions (Buttner, 2016; Topál et al., 2014) as well as cross-species synchronization of hormonal and behavioral states (e.g., Buttner et al., 2015; Duranton & Guanett, 2015; Romero et al., 2013; Ryan et al., 2019; Sümegi et al., 2014; Sundman et al., 2019). The foundation of dogs' ability to read human social behavior is their attachment bonds with humans, which are analogous to the mother–infant bond (Topál et al., 1998). When tested in adapted versions of the Ainsworth Strange Situation Test (ASST), originally developed to test attachment in children (Ainsworth & Wittig, 1969), dogs also display behavioral indicators of attachment. Dogs maintain proximity to their owners when present, use their owner as a secure base for exploring the novel environment, and display distress behavior when separated, and these behaviors are specific to their owners, as they generally do not demonstrate these behaviors with other familiar or unfamiliar humans (Cimarelli et al., 2021; Horn et al., 2013; Konok et al., 2015; Palmer & Custance, 2008; Prato-Previde et al., 2003; Siniscalchi et al., 2013; Topàl et al., 1998; Voith, 1985; Zilcha-Mano et al., 2011; for review see Udell et al., 2021). Like children, dogs can be classified into attachment styles based on their behavioral responses to the ASST: secure, insecure, avoidant, insecure ambivalent, insecure disorganized, and unclassifiable (Main & Solomon, 1986; Schöberl et al., 2016; Solomon et al., 2019). Additionally, when presented with a social or nonsocial stressor, dogs engage in social referencing, looking more at their owners than other people, and seeking proximity to their owner, often referred to as the "safe haven" effect (Cimarelli et al., 2016; Gácsi et al., 2013; Kerepesi et al., 2015; Merola et al., 2012; Rehn et al., 2017 Schöberl et al., 2016).

Studies using physiological measures of stress have offered further insight into attachment bonds between dogs and humans. In paradigms involving a social or nonsocial stressor, the presence of an attachment figure reduces physiological signs of stress (heart rate/heart rate variability: Gácsi et al., 2013; cortisol: Tuber et al., 1996; Schöberl et al., 2016). In the ASST, separation from the attachment figure evokes a physiological stress response in dogs (e.g., increases in heart rate: Palestrini et al., 2005). However, studies assessing hypothalamic–pituitary axis (HPA) activation via cortisol levels have reported inconsistent findings, which appear to vary based on several factors. Older dogs (Mongillo et al., 2013) and insecurely attached dogs (Riggio et al., 2022; Schöberl et al., 2016, 2017) experienced greater elevations in cortisol levels following the ASST, whereas dogs with separation anxiety had higher average cortisol levels that decreased throughout testing (Ryan et al., 2019).

Former shelter dogs form strong, but perhaps altered, bonds with humans despite their history of abandonment and living in a stressful environment, although they may react more anxiously to novel testing environments and humans (Cimarelli et al., 2021; Prato-Previde, 2007). The effects of other environmental influences, such as chronic early life adversity, on the attachment bonds between dogs and their owners is worthy of further exploration. Early life environments have notable effects on social buffering such that adverse rearing conditions (e.g., poor parental care, parental deprivation, peer rearing) reduce the effects of social buffering in many species. For instance, children who experience early social deprivation while being raised in orphanages do not experience the social buffering effect on HPA axis activity following interactions with their caregivers after being adopted (Hostinar et al., 2015; Wismer-Fries et al., 2008), and children with insecure attachments to their caregivers exhibit diminished stress coping and higher cortisol levels in response to separation (Gunnar et al., 1996) Similar findings are seen in other primates. Rhesus monkeys exhibited social buffering of the cortisol response when in a novel cage accompanied by a social companion, whereas those reared without a mother but in a nursery did not (Winslow et al., 2003).

Dogs who have lived in adverse and impoverished conditions can offer further insight into the role of the environment in developing attachment bonds with humans, particularly how exposure to chronic stress and a lack of socialization with humans alter the stress response. Early experimental studies established that dogs that experienced confinement, stress, and social deprivation during critical phases of development displayed behavioral abnormalities as adults, particularly fear and timidity (e.g., Beerda et al., 2000; Fox & Stelzner, 1966; Scott & Fuller, 1965; for reviews, see Dietz et al., 2018; Serpell & Jagoe, 1995). More recently, research has shown that dogs obtained from adverse or impoverished conditions, such as large commercial breeding operations that provide substandard care (often referred to as puppy mills; McMillan et al., 2011), pet stores (McMillan et al., 2013), and hoarding situations (individuals who keep large number of animals in their home under unsanitary conditions; McMillan et al., 2016) also display increased levels of social and nonsocial fear, among many other behavioral differences (for a review see McMillan, 2017). Physiological differences have been identified in these dogs as well. Dogs rescued from adverse conditions (i.e., puppy mills and hoarding situations) residing in an animal shelter exhibited significantly higher cortisol levels and more fearful behavior during interactions with an unfamiliar human than shelter dogs found as strays or surrendered by their owners (Buttner & Strasser, 2022). Among licensed commercial breeding kennels, higher hair cortisol concentrations were inversely associated with the establishment's reported socialization practices (Stella et al., 2019).

Purpose of the Present Study

No studies have yet directly explored the influence of early life adversity on the behavioral and physiological aspects of human–dog attachment. Owners have reported higher levels of attachment to their dogs, greater attention-seeking from their dogs, and separation-related problems in dogs from hoarding situations, pet stores, and puppy mills (McMillan et al., 2011; McMillan et al., 2013; McMillan et al., 2016; Pirrone et al., 2016). In the present study, we explored the social bonds between dogs rescued from adverse environments and their new owners by assessing both their behavioral and physiological responses to a mild social stressor (i.e., the threatening approach of a stranger as developed by Vas et al., 2005) while accompanied by either their owner or by an unfamiliar human. Owners also completed questionnaires about the dog's general behavior and their attachment to their dogs. Given the evidence suggesting higher cortisol levels and insecure attachment bonds in dogs from adverse life histories, we expected dogs with this background would have higher cortisol levels throughout testing relative to dogs without this known history of adversity and that the presence of the owner, rather than an unfamiliar human, would reduce cortisol levels in the dogs from adverse life histories. In addition, dogs with adverse histories would exhibit higher fearful responses to the threatening approach than dogs from the comparison group, especially when their owner was absent. If dogs with adverse histories form strong attachments with their owners, then it is predicted that they would be more relaxed, engage in high levels of eye gaze, maintain proximity and contact with their owners, and exhibit low levels of those behaviors when accompanied by an unfamiliar human. In contrast, dogs from the comparison group are predicted to engage in high levels of social and relaxed behavior overall, particularly toward their owners, and engage in more exploration in their owner's presence. Higher ratings of attachment, social and nonsocial fear, and separation-related issues are predicted in dogs from adverse histories, which are predicted to be associated with cortisol levels and the time the dogs spent in the adverse conditions.

METHOD

Participants

Dog owners were recruited by posting fliers on social media through rescue groups, shelters, and local dog clubs to study attachment in dogs from diverse backgrounds, including dogs removed from large commercial breeding facilities (CBEs) or hoarding situations due to neglect. Brief phone interviews were conducted to schedule laboratory visits and determine early life history. Exclusion criteria included dogs that were anticipated to be too fearful or possibly have an aggressive response to the procedure or dogs with chronic illnesses. Owners signed consent forms for their participation. All testing procedures were approved by the Institutional Review Board (#325-16-EP) regulations and the Institutional Animal Care and Use Committee at the University of Nebraska Medical Center (#14-044-00-EP).

We collected data from 56 dogs in total, and no dogs were excluded from data collection due to behavior. However, we did have some dogs with uncertain histories (e.g., stray dogs adopted from rescues or shelters). Those dogs were not included for analysis in the present study, resulting in a final sample size of 45 dogs belonging to six men and 39 women ($M_{\text{age}} = 44.53$, $SD_{\text{age}} = 11.73$). Twenty-three dogs were classified as having adverse early life histories including dogs removed from large commercial breeding establishments that were poorly maintained ($n = 20$), pet stores ($n = 2$), and a hoarding situation ($n = 1$). Dogs identified as coming from adverse conditions came to their new owners through rescue organizations ($n = 19$) or an animal shelter ($n = 1$). Our comparison sample of 22 typically raised dogs with no history of neglect, matched for age, sex, and size, was composed of dogs obtained from breeders operating out of their homes ($n = 9$) or farms ($n = 3$), rescue organizations ($n = 8$), animal shelters ($n = 1$), and an acquaintance's home ($n = 1$). To the owners' knowledge, dogs from the comparison group had not experienced extreme or prolonged traumatic circumstances comparable to those experienced by dogs in the adverse history group.

Subject demographics for each group are displayed in Table 1; complete characteristics of the dogs can be found in Supporting Information Table 1. No significant differences in age, weight, or sex ratio were found between groups. All but one dog was neutered. Before testing, the dogs were randomly assigned to the owner's present or owner-absent condition.

Study location

The dogs and their owners were initially brought to an office (hereafter referred to as the acclimation room) approximately 3 × 6 m in size, which contained several desks, chairs, filing cabinets, bookshelves, a water bowl, and a rug. For threatening approach testing, dogs were taken to a room approximately 5 m down a hallway from the acclimation room. The testing room was approximately 8 × 6 m and contained several desks, chairs, and bookshelves. A blanket was laid on the floor, and a low

TABLE 1 Descriptive statistics for demographic variables based on dogs' backgrounds

Variable	Adverse ($M \pm SD$)	Comparison ($M \pm SD$)
Sex (male)	39.1%	36.4%
Age (years)	7.87 ± 2.92	6.61 ± 3.62
Weight (kg)	12.98 ± 8.18	15.52 ± 11.52
Time owned (years)	4.21 ± 2.93	5.51 ± 3.75

stool was placed in the middle for the human partner to sit on during testing. A camera was placed approximately 2 m from the dog to record the dogs' and owners' behavior, which was scored at a later time.

Procedure

Acclimation phase

A schematic depiction of the procedure is represented in Figure 1. Owners and dogs were met by the primary researcher and taken to an acclimation room. The dogs were given 20 min to acclimate to the room and meet the primary researcher (both females). During this time, the protocol was described to the owner and consent was obtained from the owner. The owners were then given questionnaires to begin. Dogs could explore the room or sit with their owners throughout the acclimation period.

Social stressor

Following the acclimation period, the dogs were taken to the testing room for the stressor (i.e., threatening approach). This phase lasted approximately 10 min, including the instructions (~1 min), a 4-min prethreat observation, the threat (~1 min), and a 4-min postthreat observation. In the condition with the owner present, the primary researcher walked the owner and dog to the testing room. In contrast, in the owner's absence, the primary researcher walked the dog to the testing room while the owner stayed in the acclimation room to complete paperwork and questionnaires. Upon entering the room, the secondary researcher instructed the human partner (owner or primary researcher) to sit with the dog and hold its leash to restrict it from moving around the room. The partner, sitting on a low stool, was instructed to interact normally with the dog during the observation phases and to refrain from touching or speaking to the dog during the threatening approach.

After the 4-min prethreat observation phase, the "threatening stranger" was a secondary researcher who began the threatening approach (Vas et al., 2005). The secondary researcher (always a female) walked to the back of the room and scuffed her foot on the floor to get the dog's attention, then looked into the dog's eyes and slowly walked toward the dog with her hands behind her back with a slightly bent upper body (~5 m). The approach lasted approximately 30 s. If the dog was not paying attention to the secondary researcher, she lightly scuffed her foot on the floor or cleared her throat to get the dog's attention. The threatening approach was terminated when (1) the dog continually failed to look at the secondary researcher; (2) the dog showed severe active avoidance (e.g., trying to escape or hide); (3) the dog showed signs of reactivity, fear, or aggression (e.g., lowering head, cowering, barking, growling); (4) the secondary researcher reached the dog. Afterward, the secondary researcher walked around to the side of the room and approached the dog in a friendly manner, squatted down and spoke to the dog in a friendly voice, and reached out her hand for the dog to sniff and then pet if the dog was not displaying fearful or avoidant behavior. Following the postthreat observation, the dogs and humans returned to the acclimation room for saliva collection and to complete questionnaires. Owners were instructed to interact with their dogs as they wished.

Saliva sampling

Salivary cortisol levels have been validated as a measure of the stress response in dogs (Dreschel et al., 2014; Dreschel & Granger, 2005; Vincent & Michell, 1992). Saliva was collected from the dogs and owners at three points in 15-min intervals. After the threatening approach phase, the first sample (S1) was collected immediately upon returning to the acclimation room. Given that salivary cortisol levels will increase after approximately 15 min, S1 was expected to reflect HPA axis activity immediately before the separation and stressor, and the second sample (S2) was expected to reflect the rise and peak to the stressor (Dickerson & Kimeney, 2004), and third (S3) expected to reflect a recovery (i.e., return to baseline levels). Saliva collection with the dogs entailed placing a small piece of gauze in the dog's cheek pouch for up to 4 min until it was saturated. Mozzarella cheese was used to stimulate salivation and given to the dogs following collection.

In most cases, the primary researcher collected saliva from the dog, but in some cases, the owner elected to

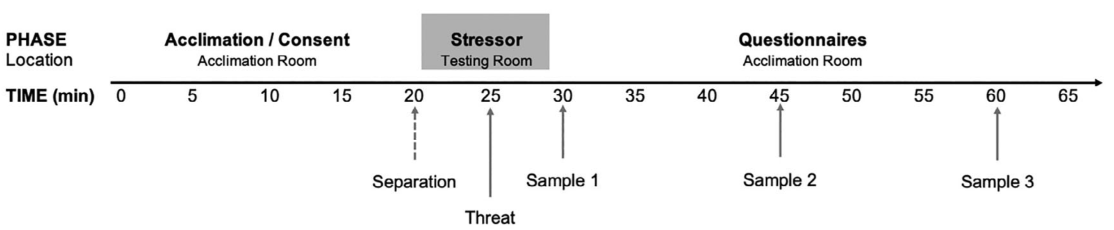

FIGURE 1 Testing sequence and timing of events

collect it. After collection, saliva was expelled into a 5-mL plastic syringe and compressed into a 1-mL centrifuge tube to ensure an adequate amount was obtained. All samples were immediately placed in a freezer and stored at −20°C until assay. All testing took place in the afternoon to control for circadian fluctuations in cortisol, and the time of testing was recorded so circadian variations could be assessed. Three dogs failed to generate adequate saliva within the 3-min period of collection for the third sample. One dog did not generate adequate saliva for the second or third sample (see Supporting Information Table 1).

Immunoassay

Upon assay, the samples were warmed to room temperature. The saliva samples were separated from residuals by centrifuging at 5,000 rpm for 5 min and then analyzed for cortisol levels using an enzyme immunoassay. The hormone assays were validated by creating displacement curves of halving dilutions from quality control saliva pools for each species. The assay is validated when hormone standards are parallel in the 10%–90% binding range such that a difference in dilution results in an equivalent difference in the calculated concentration. The saliva samples were diluted appropriately to fall in this range. Microtitre plates were coated with CORT Ab (3.6.07) to quantify cortisol, diluted to 1:25,000 in bicarbonate coating buffer, and incubated for 12 hr. The CORT standards were diluted in PBS, ranging from 1,000 to 7.8 pg/well. Labeled CORT-HRP (R4866) was diluted 1:30,000 in PBS. After the 12-hr incubation, 50 mL of PBS was added to each well, followed by 50 mL of the saliva samples or cortisol standards. After 50 mL of HRP was added, the plates were incubated for 2 hr. Free and bound hormones were separated, after which an enzyme immunoassay substrate (ABTS, H_2O_2) was added. Absorbance at 405 nm was measured in a microplate reader. Samples from the same individual were tested on the same plate in duplicate. The intra- and interassay coefficients of variation were 7.67% and 12.92%, respectively.

Measures

Behavioral scoring

From the videos of the testing phase, the behavior was coded using a continuous recording of dogs' behavior during the 4-min periods before and after the threatening approach. During the threatening approach, the dogs' general responses were coded as fearful, reactive, friendly, or neutral, and gaze alternations (see ethogram in Table 2) between the threatening stranger and social partner were also recorded. Two blind observers independently scored each subject's behavior using Stopwatch+ software. An average score was derived for each dog between the two observers' scores for data analysis. Interrater reliability was excellent (ICC = .93).

TABLE 2 Ethogram of observed behaviors in dogs during social interactions

Behavior	Description
Response to threatening approach	
Reactive	Growling, barking, lunging
Fearful	Ears back, lowering head, tucking tail between legs, cowering, averting gaze, trembling, hiding, escaping
Friendly	Tail-wagging, movement towards stranger
Neutral	No change in behavior
Gaze alternation	Staring, looking at, or head frontally oriented back and forth from the stressor to social partner at any point during threatening approach
Behavior during entire testing phase (duration)	
Human-directed eye gaze	Staring, looking at owner/partner or no clear gaze direction but head frontally oriented to owner/partner
Initiating contact	Sniffing, licking, gentle touching with the nose or paw, play bouts, and body contact (i.e., the subject rests or stands up in physical contact, excluding tails, with his/her owner or partner) with or without solicitation from owner/partner
Close proximity	Dog is within arms' reach of the social partner
Relaxed behavior	Calm with no visual evidence of anxiety; tail is in neutral or low position if standing; includes playful behavior
Exploration	Movement of snout along objects and/or clear sniffing movements exhibited

Questionnaires

Throughout testing, owners were asked to complete several forms and questionnaires to gain insight into their dogs' behavior and their relationship with the dog. A background form contained questions about the owner's age and gender, dog's age, breed, sex, number of other dogs in the household, when and how the dog was obtained, any behavioral or medical issues the dog has had, medications the dog is on, and any rehabilitation they have done with the dog.

Owners also completed the Canine Behavioral Assessment Research Questionnaire (C-BARQ, Hsu & Serpell, 2005), a research tool that assesses an array of behavioral characteristics and has been used in a range of dog populations (e.g., Duffy et al., 2008; Duffy & Serpell, 2012; McMillan et al., 2011; Van den Berg et al., 2010). The questionnaire contains 100 items in which owners are asked to rate their dogs' behavior in various situations on a scale from 1 to 5. The C-BARQ comprises 14 subscales generally about trainability, aggression, fear, attachment, attention seeking, excitability, and separation-related behavior, which are calculated as the mean of the questions on that subscale as 22 miscellaneous items. A score of 0 reflects the absence of behavior. In contrast, a score of 4 indicates an intense or frequent behavior, with higher scores generally indicating a problem behavior except for questions about trainability. Owners completed the online version of the C-BARQ (http://vetapps.vet.upenn.edu/cbarq/) during the acclimation phase of testing on a desktop computer.

A 23-item questionnaire regarding owners' relationships with their dogs was also given to owners to complete. The questionnaire included a shortened version of the Monash Dog Owner Relationship Scale (MDORS; Dwyer et al., 2006), containing a total of 19 items from the three subscales: Dog-Owner Interaction (five items, e.g., "How often do you hug or kiss your dog?"), Perceived Emotional Closeness (nine items, e.g., "My dog provides me with constant companionship"), and Perceived Costs (five items, e.g., "How often do you feel that having a dog is more trouble than it is worth?"). The rating scales ranged from 1 (*Never*/*Strongly disagree*) to 5 (*At least once a day*/*Strongly agree*). Additionally, four items from the Lexington Attachment to Pets Scale (Johnson et al., 1992) were also included (i.e., "My pet knows when I am feeling bad," "I believe that loving my pet helps me stay healthy," "My pet and I have a very close relationship," and "My pet makes me happy"). These items were also rated on a scale from 1 (*Strongly disagree*) to 5 (*Strongly agree*).

Data analysis

The data were analyzed using R Studio Version 1.2.5001 (aligned rank transformation analyses of variance [ANOVAs]) and IBM SPSS Statistics version 24 (all other nonparametric analyses). Cortisol was evaluated in three manners: mean cortisol levels were calculated by taking the average of all samples for each dog, calculating changes in cortisol levels from the first to second sample (S1 to S2), and calculating changes in cortisol levels from the first to third sample (S1 to S3). For behavioral observations during social interactions, durations spent in each behavior in the 4 min before and after the threatening approach were combined for data analysis. Given the sample sizes and data skewness, nonparametric analyses were used. Aligned rank transformation ANOVAs (Leys & Schumann, 2010; Wobbrock et al., 2011) tests were used to compare cortisol levels and behavioral variables between dogs from different backgrounds in each condition. Relationships between behavioral variables and cortisol levels (mean, changes from S1 to S2, and changes from S1 to S3) were evaluated using Spearman rank correlations. A chi-square test for independence was used to assess differences in behavioral responses to the threatening approach based on background and condition. Due to low occurrence rates, gaze alternation during the threatening approach was recoded from a continuous (frequency) variable into a dichotomous variable (present or not present) and then evaluated between conditions and backgrounds using a chi-square test for independence. A Kruskal–Wallis test was performed to assess differences in cortisol levels (mean, reactivity S1 to S2, and recovery S1 to S3) based on dogs' general responses to threat (see Table 2 for operational definitions for reactive, fearful, friendly, and neutral). Owner-reported data from several questionnaire subscales (MDORS Emotional Closeness and all C-BARQ subscales) were compared between dogs based on the background using nonparametric Mann–Whitney U tests. Relations between cortisol levels (mean, changes from S1 to S2 and changes from S1 to S3) and owner-reported data were evaluated with Spearman rank correlations. Spearman rank correlations also evaluated associations between time spent in adverse conditions with cortisol levels and C-BARQ subscales. All analyses used a significance threshold of $\alpha < 0.05$ (two-tailed).

RESULTS

Physiological and behavioral responses during testing

Cortisol levels

Overall, the dogs' cortisol levels did not change throughout the test, $p > 0.05$. An equal number of dogs experienced increased cortisol levels from S1 to S2 (increase: 50%; decrease: 50%). A decrease was found in 44% and an increase in 56% of the dogs from S1 to S3; the same percentages were also found in changes from S2 to S3.

The dogs' mean cortisol levels did not differ significantly based on condition or background alone, nor was there an interaction between the variables, $p > 0.05$. Dogs from adverse backgrounds, regardless of condition, exhibited marginally greater decreases in cortisol levels from S1 to S2 than dogs from the comparison group, $F(1, 40) = 3.78$, $p = .059$, $\eta_p^2 = 0.09$ (see Figure 2a), and significantly greater decreases in cortisol levels from S1 to S3, $n = 41$, $F(1, 37) = 5.85$, $p = .021$, $\eta_p^2 = 0.14$ (see Figure 2b).

Behavioral observations

A significant interaction was found between condition and background on exploratory behavior, $F(1, 39) = 4.20$, $p = .047$, $\eta_p^2 = 0.10$. Dogs from the comparison group spent more time engaging in exploratory behavior in the owner-present condition than in the owner-absent condition, $p = .007$, whereas dogs from adverse backgrounds showed no difference between conditions, $p > .05$ (see Figure 3a). Regardless of background, dogs in the owner-present condition spent more time initiating contact with their owner than dogs in the owner-absent condition with the unfamiliar human, $F(1, 40) = 5.25$, $p = .027$, $\eta_p^2 = 0.12$ (Figure 3b).

A significant main effect for the condition was on relaxed behaviors, $F(1, 39) = 12.27$, $p < .001$, $\eta_p^2 = 0.24$. The dogs engaged in more relaxing behaviors when their owners were present overall. There was a trend for an interaction between background and condition for relaxed behaviors, $F(1, 39) = 3.44$, $p = .07$, $\eta_p^2 = 0.08$. Dogs from adverse conditions engaged in more relaxed behaviors when their owner was present compared with when their owners were absent and with an unfamiliar human (see Figure 3c).

Response to a threat

Regardless of condition, responses to the threatening stranger differed between dogs based on their backgrounds, $\chi^2(3, 45) = 12.61$, $p = .006$. Dogs from adverse conditions most often displayed fearful responses and least often showed reactive behavior (adverse: fearful: 47.8%, reactive: 8.7%, friendly: 21.7%, neutral: 21.7%), whereas dogs from the comparison group primarily exhibited friendly or reactive responses and least often displayed fearful behavior (comparison: fearful: 4.5%, reactive: 36.4%, friendly: 36.4%, neutral: 22.7%). When examined by condition, dogs from adverse backgrounds also responded similarly to the threatening stranger regardless of whether their owner was present, most often exhibiting fearful behavior, $p > .05$ (Figure 4a). However, dogs from the comparison group displayed different behavior based on the experimental condition. Comparison dogs in the owner-present

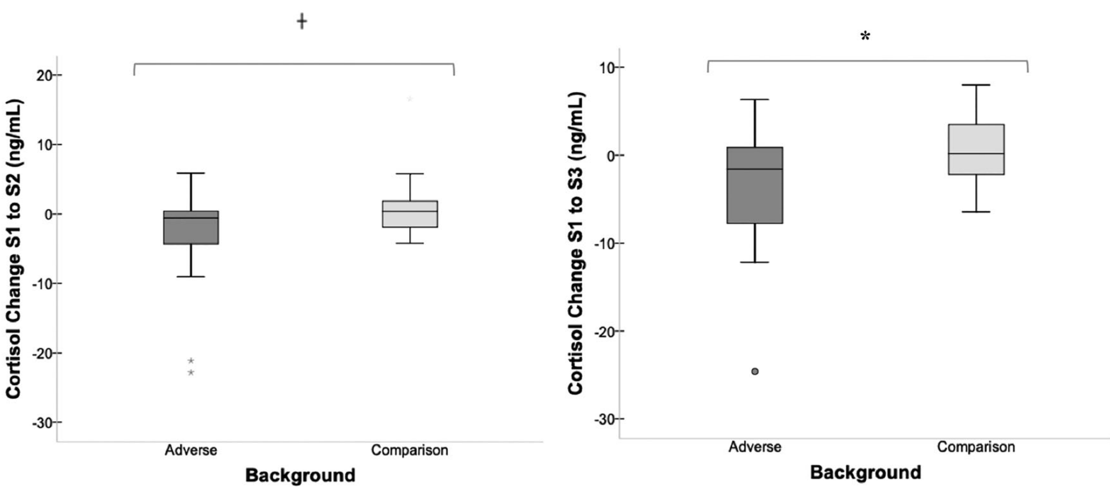

FIGURE 2 Change in cortisol levels between (a) Samples 1 and 2 and (b) Samples 1 and 3 based on dogs' backgrounds. Medians are indicated by horizontal lines in box, interquartile ranges indicated by boxes, ranges excluding outliers indicated by whiskers, and outliers indicated by circles. Brackets and a large asterisk indicate significant differences; a cross indicates a marginal trend.

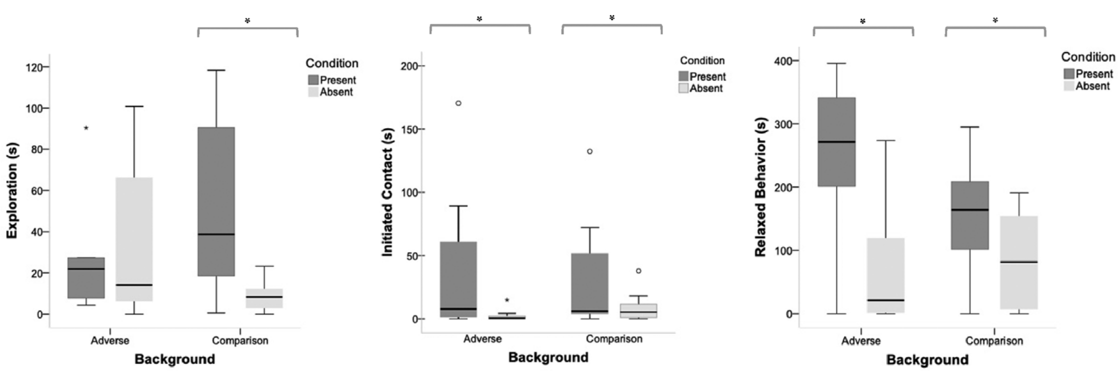

FIGURE 3 Duration of time engaging in (a) exploration, (b) initiating contact, and (c) relaxed behavior based on background and experimental condition. Medians indicated by horizontal lines in box, interquartile ranges indicated by boxes, ranges excluding outliers indicated by whiskers, outliers indicated by circles, and extreme values indicated by small asterisks. Brackets and large asterisks indicate significant differences.

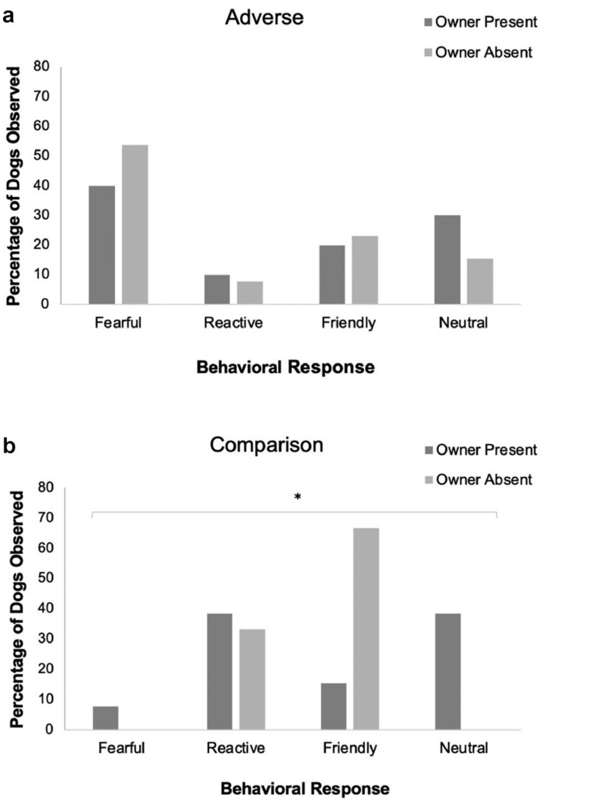

FIGURE 4 Behavioral responses to threatening approach based on experimental condition among dogs from (a) adverse backgrounds and (b) comparison group. Brackets and large asterisks indicate significant differences.

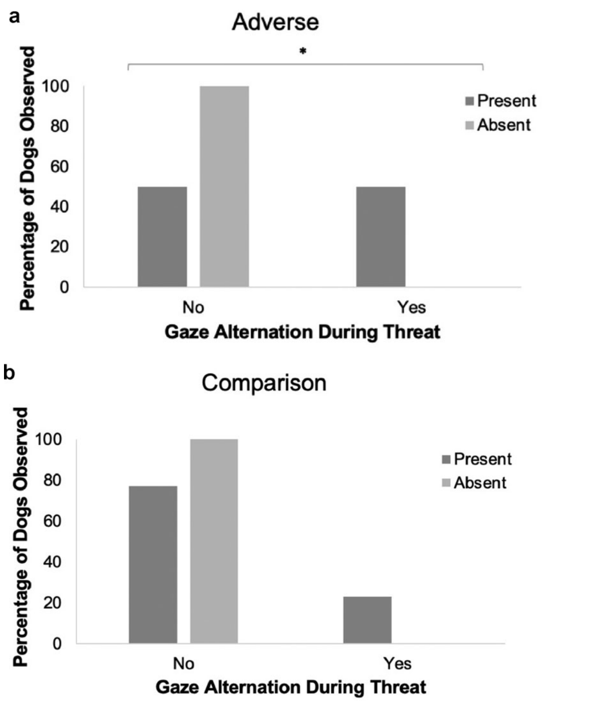

FIGURE 5 Presence of gaze during the threatening approach based on experimental condition among dogs from (a) adverse backgrounds and (b) comparison group. Brackets and large asterisks indicate significant differences.

condition exhibited a range of responses, primarily reactive and neutral. In contrast, comparison dogs in the owner-absent condition exclusively displayed a friendly or reactive response to the approach, $\chi^2(3, 22) = 8.04$, $p = .045$ (Figure 4b). We found no differences in cortisol levels based on dogs' responses to the threatening approach, $p > .05$.

During the threatening approach, dogs from adverse histories engaged in gaze alternation with their owners more often than with the unfamiliar person (owner present: alternated gaze: 50%, did not alternate gaze: 50%; owner absent: alternated gaze: 0%, did not alternate gaze: 100%), $\chi^2(1, 23) = 8.31$, $p = .004$, whereas dogs from the comparison group showed no significant differences in gaze alternation between conditions (owner present: alternated gaze: 23%, did not alternate gaze: 77%; owner absent: alternated gaze: 0%, did not alternate gaze: 100%), $p > .05$ (Figure 5).

Owner-reported data

Responses to the MDORS Emotional Closeness subscale did not differ among owners of dogs from adverse backgrounds and owners from the comparison sample (adverse: $Mdn = 4.67$; comparison: $Mdn = 4.33$), $p > .05$. Analysis of owners' responses on the C-BARQ revealed that dogs from adverse conditions displayed significantly higher levels of stranger-directed fear, nonsocial fear, separation-related problems, and attachment and attention seeking but lower levels of trainability and chasing (see Table 3). Dogs' mean cortisol levels and changes in cortisol levels throughout testing were not correlated with the C-BARQ scales considered relevant to this study (i.e., stranger-directed fear, nonsocial fear, separation-related problems, and attachment and attention seeking), $p > .05$. However, changes in cortisol levels between S1 to S3 were significantly correlated with reported nonsocial fear, $rho(41) = -0.342$, $p = 0.029$, and touch sensitivity, $rho(41) = -0.343$, $p = 0.028$, suggesting that lower change in cortisol across testing was associated with more nonsocial fear and touch sensitivity (Figure 6).

Time spent in adverse conditions, measured in months since birth until adopted or rescued, was not correlated with cortisol levels, $p > .05$, but was significantly correlated with the following C-BARQ subscales: Training, $rho(23) = -0.414$, $p = .050$, Dog Aggression, $rho(23) = -0.586$, $p = .004$, and Stranger-Directed Fear, $rho(23) = 0.421$ $p = .045$, suggesting that the more time in the adverse condition was associated with lower training ability and less dog aggression but more stranger directed fear.

TABLE 3 C-BARQ results based on dogs' background

Subscale	Adverse (*Median*)	Comparison (*Median*)	n	U	p	r
Trainability	**2.13**	**2.63**	**44**	**115.0**	**.003**	**.45**
Stranger-directed aggression	0.30	0.60	45	187.5	.135	.22
Owner-directed aggression	0.00	0.00	44	218.5	.529	.09
Dog-directed aggression	0.67	0.88	44	217.0	.554	.09
Family dog-directed aggression	0.25	0.25	43	230.0	.980	.00
Dog-directed fear	1.00	0.63	43	153.0	.056	.29
Stranger-directed fear	**1.33**	**0.38**	**45**	**139.0**	**.008**	**.39**
Nonsocial fear	**2.00**	**0.50**	**45**	**75.0**	**.000**	**.60**
Touch sensitivity	0.75	0.63	45	212.0	.348	.14
Separation-related problems	**1.13**	**0.57**	**45**	**138.5**	**.009**	**.39**
Excitability	2.50	2.25	44	226.5	.715	.06
Attachment and attention seeking	**2.67**	**2.09**	**45**	**150.5**	**.020**	**.35**
Chasing	**1.25**	**2.63**	**41**	**121.5**	**.021**	**.36**
Energy	2.00	2.00	45	229.5	.588	.08

Note. Mann–Whitney *U* test: *r* between 0.3 and 0.5 indicated a medium effect size.

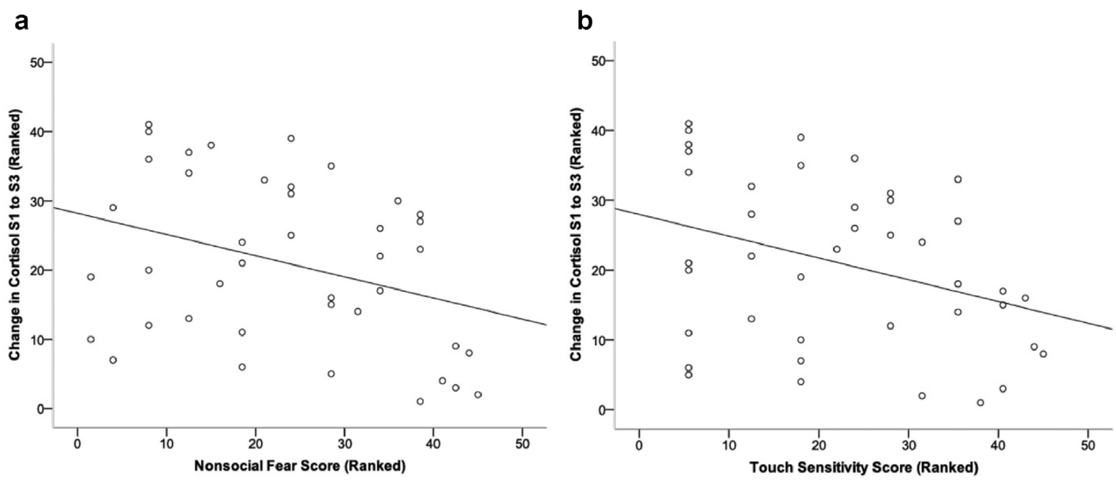

FIGURE 6 Scatterplots depicting nonparametric Spearman Rho correlations between change in cortisol from S1 to S3 and (a) C-BARQ Nonsocial Fear Score and (b) C-BARQ Touch Sensitivity Score

DISCUSSION

This study explored behavioral and physiological differences in dogs with histories of adversity by evaluating the stress-buffering effect of their owners' presence during a social stressor. The results of this study confirm previously described owner-reported differences in attachment and fear behavior in dogs from adverse backgrounds, providing physiological and behavioral evidence that early life adversity intensifies social and nonsocial fear, which may then influence social bond formation.

Although the dogs' cortisol levels remained primarily stable throughout testing, dogs from adverse histories exhibited greater decreases in cortisol levels between the first and last samples, suggesting a stress-buffering effect which is typically not observed in all dogs but in specific subgroups of dogs (Gácsi et al., 2013; also see meta-analysis by Bunea et al., 2017). For example, securely attached dogs exhibited greater cortisol reactivity to a threatening stranger than dogs classified as insecurely disorganized (strong approach-avoidance conflict or fear on reunion) in their owner's absence (Schöberl et al., 2016). Similar patterns have been shown in studies using the ASST, with cortisol levels increasing during testing more often in insecurely attached dogs as opposed to securely attached dogs (Riggio et al., 2022; Schöberl et al., 2016) as well as with older dogs than with younger dogs (Mongillo et al., 2013; Schöberl et al., 2016). Although our findings may reflect different attachment types, it is also possible that dogs from adverse histories, having higher ratings for stranger-directed fear and displaying more fearful behavior toward the threatening stranger, were more affected than the comparison dogs (Cimarelli et al., 2021). Alternatively, the unfamiliar human may serve as a stress buffer for dogs from the comparison group just as well as their owners. However, our behavioral observations and the findings of previous studies (e.g., Cimarelli et al., 2021) are inconsistent with this possibility.

Dogs from adverse backgrounds displayed several behaviors indicating they used their owner as a safe haven during testing (Cimarelli et al., 2016; Gácsi et al., 2013), including engaging in higher levels of initiating contact, relaxed behavior, and more gaze alternation in response to the threat when with their owners. Initiating contact and eye gaze with their owners may indicate that these dogs found the novel situation stressful and sought attention to regulate their emotional responses (Nagasawa et al., 2015). Dogs from our comparison group explored when in their owners' presence more than unfamiliar humans', illustrating the secure base effect in attachment bonds (Palmer & Custance, 2008). In response to the threatening stranger, dogs with adverse histories mostly responded fearfully regardless of whether their owners accompanied them. In contrast, the comparison dogs most often exhibited reactive or friendly reactions, with more friendly responses when accompanied by an unfamiliar human. Previously, Gácsi et al. (2013) found that only dogs that responded reactively (i.e., growled and/or barked) toward the threatening stranger exhibited concurrent increases in heart rate and decreased heart rate variability, which was attenuated by their owners' presence. However, we found no differences in cortisol levels based on dogs' behavioral responses to the threatening approach, nor did we find associations between dogs' behavior with their cortisol levels.

Dogs from adverse backgrounds engaged in more social referencing with their owners, as indicated by greater rates of gaze alternation between the stressor and their owner during the threatening approach. Social referencing with an owner or parent has been proposed to seek comfort and gather information about an ambiguous or threatening situation (dogs: Rehn et al., 2017; children: Corriveau & Harris, 2009; Main, 2000; Stenberg & Hagekull, 2007; Walden & Kim, 2005). In our study, the comparison dogs did not demonstrate social referencing, even though many of these dogs displayed reactive responses to the threatening approach. Given their higher levels of social fear, perhaps dogs from adverse backgrounds might engage in more gaze alternations to gather information about a stressor they perceive as threatening. Dogs without this history focused more on the stressor and relied less on their owner for information and comfort.

In this study, as in previous ones (McMillan et al., 2011; McMillan et al., 2013; McMillan et al., 2016), owners reported higher separation-related issues, attachment to their dog, and attention-seeking in dogs with adverse histories. Interestingly, dogs in our study with adverse histories exhibited similar cortisol trends as dogs with separation anxiety reported by Ryan et al. (2019), showing higher average cortisol levels that decreased during the ASST. This pattern of altered attachments and more separation-related problems is consistent with studies of dogs from other adverse situations (e.g., Flannigan & Dodman, 2001; Overall et al., 2000), which has led some to suggest that adversity amplifies the dogs' bonds with their owners, which can lead to separation-related distress (Serpell & Jagoe,1995). Yet, it is debated whether separation-related problems are the results of a type of "hyperattachment" (e.g., Sherman, 2008) or rather are indicative of insecure attachments (McMillan et al., 2016) or some alternative attachment pattern (Parthasarathy & Crowell-Davis, 2006). Further research may help determine whether dogs from adverse environments can be considered hyperattached to their owners, fall into an insecure or alternative attachment style, or whether their increased fear behaviors are responsible for the differences observed.

Intriguingly, dogs from adverse histories can form intense bonds with humans despite the impoverishment they experienced. In animal models as well as in humans, early life adversity (e.g., parental deprivation, low maternal care, child abuse or neglect, impoverished environments, chronic stress exposure) has consistently been shown to reduce the social buffering effects between caregivers and their young (Nachmias et al., 1996; Raineki et al., 2014). For instance, internationally adopted children who had experienced institutional care show no dampening effect on their cortisol responses when accompanied by their adoptive parents (Hostinar et al., 2015) and, in some cases, even display higher cortisol levels after interacting with an adoptive parent as opposed to a stranger (Wismer-Fries et al., 2008). Postinstitutionalized children have also been shown to display less secure and more disorganized attachments than nonadopted peers (van den Dries et al., 2009) and indiscriminate friendliness and a lack of social restraint around strangers (Chisholm, 1998; Lawler et al., 2014; O'Connor et al., 1999; Roy et al., 2004; Rutter et al., 2007; Zeanah et al., 2002). Thus, dogs with similar early life adversity exhibit the opposite outcomes of children in analogous settings. However, a selection bias may exist in testing dogs adopted into human homes. Only the most social and resilient dogs may be selected as rehoming candidates and adopted. Given that dogs have been suggested as a potential model species for behavioral genetics due to their similar sociocognitive and emotional systems (Hall & Wynne, 2012; O'Brien & Murphy, 2003), exploring gene–environment interactions in dogs could offer insight into resilience following early life and chronic adversity.

In the present study, dogs that spent longer durations in adverse conditions were reported by their owners as being less trainable, less aggressive toward dogs, and more fearful of strangers. Unlike owner-reported behavioral outcomes, dogs' time in adverse conditions was unrelated to their cortisol levels. However, our results are consistent with previous research that dogs rescued from adverse environments in an animal shelter displayed higher salivary cortisol levels, more fearful behavior, and less affiliative behavior during social interactions with an unfamiliar human than a comparison group of dogs (Buttner & Strasser, 2022). A previous study of dogs residing in licensed commercial breeding kennels also found higher hair cortisol concentrations (a measure of chronic stress) were inversely associated with the establishment's reported socialization practices (Stella et al., 2019). Dogs living in adverse conditions are exposed to chronic stress (McMillan, 2016), which elicits a prolonged stress response, eventually leading to excessive release of glucocorticoids and stress-induced dysregulation of the HPA axis (Hennessy et al., 2006; Hennessy et al., 2002). Prolonged stress throughout sensitive windows of development, as well as prenatally, causes changes to the neural structures and pathways involved in the stress response, including a larger and more responsive amygdala (i.e., the limbic area responsible for the fear response; Bonne et al., 2004; Dettling et al., 2002; Levine, 1957; Lupien et al., 2009; Mangiavacchi et al., 2001), and programs the HPA axis to hyper-, or sometimes, hyporesponsiveness to stress-provoking stimuli (Gunnar & Quevado, 2006; Heim et al., 2000). Thus, the severity of the conditions in which dogs are reared and maintained, the timing of exposure to these conditions, and the length of time spent in those conditions may influence HPA axis activity and behavioral outcomes.

Conclusion

The findings from this study provide further insight into how early life histories influence biological systems that underlie the dogs' social behavior. From an applied perspective, studies like ours could inform on the care and rehabilitation of dogs removed from adverse environments due to neglect and call attention to the detrimental effects. Though isolating one specific contributor to the altered physiological and behavioral outcomes of dogs from adverse environments is nearly impossible, reducing overcrowded housing situations, implementing adequate human socialization, environmental enrichment, gradually weaning puppies from their mothers at a proper age, and providing quality medical care and nutrition could mitigate these effects.

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CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to disclose.

ETHICS APPROVAL

This research was approved by the review board associated with the University of Nebraska at Omaha (protocol #14-044-06).

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