


Resilience In Dogs? Lessons From Other Species

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Abstract: What are the key factors of psychological resilience in dogs? Why do some individuals recover swiftly from neglect, abuse or several years of harsh kennel environments, while some seem to be permanently traumatized by much milder adverse experiences? Resilience is a concept seldom discussed in canine studies; however, many studies have identified risk factors (both environmental and genetic) for developing anxieties, aggression or other behavioral problems. These studies also indicate several factors that may act as protective agents against life adversities. In this paper, I will present some of the most commonly identified key factors of resilience in other species and discuss what has been found in dogs. This paper is an attempt to raise focus on the positive key factors in a dog's life that are important for dog welfare, a healthy psychological outcome and are also important building blocks of a happy and well-behaving pet.

Keywords: resilience, dog, stress

Introduction

The concept of resilience has been used in several scientific fields, for example in ecology, engineering, environmental sciences, social sciences, economics, and psychology.¹ Resilience has many definitions depending on the studied system; however, a shared aspect in all the definitions is the ability to bounce back after adversity.¹ Resilience in this study is defined as reduced vulnerability to unfavorable experiences, the ability to overcome adversity or stress, or a good outcome despite negative experiences.² Resilience is a dynamic process that maintains or regains homeostasis in conditions of stress,³ and several protective key factors have been found. Psychological resilience has been mostly studied in humans, and laboratory animals. In humans, the concept of resilience is often discussed together with the risk of psychiatric disorders. In this review, I discuss resilience against canine behavioral problems, such as various anxieties and aggressiveness. In dogs, many studies have investigated predisposing risk factors (both environmental and genetic) for anxiety and aggression, however, fewer studies have focused on the factors supporting healthy psychological development and good behavioral outcomes.⁴ Understanding both risk factors and supporting factors for canine resilience is, however, an important part of dog welfare. In this paper, I will review the key factors of resiliency that have been found to be important in other species, and discuss the evidence found in canine studies.

Neurobiology Of Resilience

The neurobiology that mediates stress response and reward experience is also important in the neurobiology of resilience.⁵ While acute stress responses promote

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adaptation and survival, chronic stress can promote pathophysiology.⁵ Studies done both in animals and humans, suggest that fast activation and efficient termination of the stress response are both associated with resilience.⁵ Resilience can also be either passive or active.⁶ Passive resilience is the absence of certain key molecules which affects negatively individual's coping ability, whereas active resilience means that individual has specific molecular adaptations, that promote resilience.⁶

Several neurotransmitters, hormones and neuropeptides are associated with the stress response.⁵ Differences in their function, and also differences in the interaction between these factors are partly responsible for the large observed variability between individuals in stress resilience.⁵ In addition to the hypothalamic-pituitary-adrenal axis (HPA), the sympathetic nervous system (SNS) and the glutamatergic, dopaminergic and serotonergic neurotransmitter systems are involved in the stress response.^{3,6} Hippocampus is modulated by stress hormones and is very vulnerable to the impact of stress.⁷ Hippocampus is also one of the main brain areas controlling HPA axis.⁷ Other brain area having a strong control over stress pathways is medial prefrontal cortex (mPFC).⁷ Brain is a dynamic organ, showing great plasticity throughout the life.⁸ Future research aims to identify the biological changes behind flexible adaptation.⁸

Broad and deep knowledge from neurobiology is outside the scope of the present paper but is nicely reviewed, for example, in McEwen et al (2015)⁸ and in Liu et al (2018).⁷

Personality

Personality differences may partly explain how individuals deal with stressors.⁹ Neuroticism is a personality trait, where individuals with high neuroticism scores are more likely to experience emotions such as anxiety and fear.⁹ A recent meta-analysis found that human resilience correlated negatively with personality trait Neuroticism and positively with Extraversion, Openness, Agreeableness, and Conscientiousness.¹⁰ This study suggested that in humans, positive emotions, self-control, emotional stability and social activity are the core elements of resilience.¹⁰ How important are these individual characteristics compared to environmental factors? Some human studies suggest that resilience is more associated with individual personality traits compared to other important factors such as social relationships, environmental factors, and even maltreatment.¹¹ It has even been suggested that in humans,

neuroticism and extraversion are reliable predictors of resilience.^{10,11} Dog personality research has identified several personality categories that correspond closely to human personality traits. In dog personality studies, the traits Fearfulness (related to Neuroticism), and Sociability (or Extraversion) are the most frequently emerging personality traits.¹²⁻¹⁵ In dogs, a high degree of fearfulness is often already considered as pathological and problematic. Fear is a fundamental emotion, which is needed for an individual to survive.¹⁶ However, it may become pathological if it is prolonged and generalized. A clear correlation between different anxieties (for example noise fear, separation anxiety and fearfulness)¹⁷⁻¹⁹ also exists, suggesting that a fearful personality may predispose the dog to other anxieties, and to stereotypic behavior.²⁰ A very fearful individual may never recover from a traumatic experience.

Interestingly, resilient children seem to have personality characters that raise positive responses from other people.²¹ In children, good self-regulation and an easy-going temperament have been found to be protective factors in resilience.²² Inhibitory control has recently gained a lot of attention in canine research. In dogs, impulsivity has been shown to be a stable trait over time²³ and high impulsivity has been suggested to predict behavior problems in dogs.²⁴ In people with anxiety disorders, the emotional regulation is thought to be disrupted.²⁵ The heart rate variability (HRV) has been found to be associated with the ability to regulate emotions – low variation reflecting low ability to regulate emotions.²⁵ In dogs, fearful and aggressive dogs with problem behaviors have been found to have low HRV,²⁵ indicating that high HRV might increase resilience in dogs.

In dogs, a high level of boldness, sociability and emotional and inhibitory control, together with the ability to adapt to change and show flexibility are most likely crucial parts of resilience. Although studies investigating resilience after traumatic experiences in dogs are still lacking, some indications supporting this claim can be found. Bold dogs (compared to shy dogs) had better resistance to diseases in a dog shelter, which is a stressful and very infectious environment.²⁶ As boldness and sociability differ between different breeds,²⁷⁻²⁹ could it also be interpreted that some breeds are more resilient in facing adversities compared to others? The Labrador is among the boldest and most social (extraversion) dog breeds studied¹² and is also the most popular dog breed as a family pet in several countries, as well as highly used also as a working dog. One might suspect that the ability to adapt and recover from negative

experiences may be one of the important qualities behind this breed's popularity. However, large-scale breed-wise studies are mostly lacking, and only few breeds are studied intensively. The observation that small dogs have more various problem behaviors compared to larger sized dogs,³⁰ and furthermore, also have predisposing genetic factors for fear and aggression³¹ also suggests that large-sized dogs may have better resilience.

Positive emotions and optimism seem to be very beneficial for human psychological health as these traits protect against stress.³² Emotional states (or more permanent personalities) have been measured from dogs using either a cognitive bias or a lateralization paradigm, and dogs with separation anxiety or with possible pain, have been more pessimistic in these studies.^{33–35} As dogs also seem to differ in trait optimism, can we assume that more optimistic dogs are more resilient? A recent study found a connection between personality and cognitive bias: sociable and excitable dogs were more optimistic (however, also dogs having non-social fear were more optimistic).³⁶ Dogs with separation-related behavior and dog-dog aggression/fear were more pessimistic.³⁶ In humans, in addition to emotional states, also individual personality traits are associated with the cognitive processing of various environmental stimuli.³⁷ People scoring high on neuroticism-trait tend to make more pessimistic judgements and assess the ambiguous stimuli more negatively, compared to people having low neuroticism scoring.³⁷ Sociable and excitable dogs might be more optimistic in their interaction with environment, and these personality traits may act as protective factors when facing adverse experiences.

Environmental Factors

Maternal Care

Individual and natural variation in maternal styles observed in humans, primates and rodents is associated with divergent recovery from stress.^{1,2} Rodent studies have shown that good quality maternal care (high levels of grooming and licking, and arched-back nursing) results in offspring that are less anxious, have lower corticosterone levels after stressful experience and have higher level of glucocorticoid receptor expression in the brain, not only as juveniles, but also in adulthood.³⁸ These changes can be seen even after several generations and are thus transgenerational.³⁸ In dogs, good quality maternal care has been found to be associated with offspring having: less fearfulness,³⁹ less stereotypic behaviour,²⁰ decreased stress reaction in novel situation,⁴⁰ and increased sociability, persistency and

playfulness.⁴¹ Thus, there seems to be a good amount of evidence that good maternal care in dogs is an important factor in increasing individual resilience.

Good-caring rodent mothers have female offspring that also show good maternal care, probably due to transgenerational epigenetic effects.³⁸ Maternal behavior has also a heritable component⁴² and some studies have observed that the maternal care varies across different breeds in other domesticated species.⁴³ Therefore, it may well be that also dog breeds differ in maternal behavior.³⁹ While breeding has produced extensive variation in morphology and behavior between different dog breeds, it may have also cause relaxed selection on maternal care in some breeds.³⁹ This has not, however, been thoroughly studied in dogs. In other domesticated species, severe defects in maternal behavior have been observed.⁴³ Natural and possibly even breed-related variation in maternal care (mediated via epigenetic or/and genetic factors) may have a large effect on variation in anxiety in dogs.

Early Life Stressors, Other Adversities And Growing Environment

In rodents, an early growing environment which is lacking appropriate social, emotional or sensory stimulation may lead to brain circuitry malfunctioning.⁴⁴ Correspondingly, an enriched early environment can have several positive effects, e.g. increase in brain weight as well as increases in the density and number of blood vessels.⁴⁴ Enriched environment was also found to associate with increases in dendritic elements, gene expression, synapses, neuron soma size, and glia in the brain.⁴⁴ More enriched environment in rodents during development seems to buffer against stress later in life.⁴⁵ Also, in dogs, enriched early environment⁴⁶ and good puppy socialization³⁹ have been shown to decrease anxiety. Enrichment of the early environment at the age of 3–5 weeks may have long-lasting effects on the dog's ability to cope with novel situations.⁴⁷ Allowing puppies to watch video images at the age of 3–5 weeks decreased neophobia,⁴⁷ and an early enrichment protocol for puppies results in less anxieties as adults.⁴⁶ Also, adoption at the age of eight weeks seems to have the best behavioral outcome for dogs.⁴⁸ Experiences and life events during 3–12 weeks of age (known as sensitive period) have large and long-lasting effects on adult behavior,⁴⁹ and thus adoption at the age of eight weeks allows the dog to socialize properly to its new home and living environment.

A high number of adverse life events may have a negative effect on the resilience. In dogs, for example, if the dog is acquired from a rescue center or a pet shop, it has an increased risk for several behavioral problems, including aggression and fear.^{50,51} A kennel environment and the loss of an owner are most likely highly traumatic experiences for the majority of dogs and cause high levels of anxiety – as much as 68% of rescue dogs were reported to be very fearful by their new owners.⁵⁰ In addition, for being harsh environments, kennels and pet shops have also other factors which may predispose to anxiety. Many dogs are abandoned into the kennels because they already have behavioral problems, and many pet shop puppies might originate from puppy mills, where dog's personality is seldomly used as a major breeding criterion.⁵¹ Increasing the human-dog interaction may reduce the cortisol response of dogs in the harsh shelter environment,⁵² and thus may work as a resilience factor for shelter dogs. Questionnaire data recently showed that dogs with sensory or health problems at older age had more likely experienced a traumatic event during their life.⁵³ As a traumatic event for the dog, the owners listed the following events: time spend at a dog shelter, change of owner, suffering a traumatic injury, having a prolonged disease or surgery, being lost (run away) for a time, and change in family structure.⁵³

Adversity may, however, work also as a positive factor. Resilience may be strengthened by risk experiences that lead to successful coping.⁵⁴ In animal studies (squirrel, monkey and rodents) brief mother – infant separations may produce decreased reactivity to stress when tested later in novel situations.⁵⁵ Some evidence also exists from dogs; brief separation and handling of puppies increase emotional stability and reduce stress reactivity,⁵⁶ and several breeders are already using this kind of early gentling protocol for newborn puppies. In children, successful happy separations (staying with grandparents or sleepovers with friends) seem to increase resilience when facing unhappy separations (e.g. hospitals) later in life.⁵⁴ Dogs are often taken to kennels for periods of their owner's vacation or travel, which can be a serious stressor for some individuals. Could similar “happy separations” and staying for short periods with familiar people support the dog's resilience when facing time in kennels?

Attachment And Social Relationships

In humans, the attachment between the child and the caregiver is a crucially important source of resilience.³ Attachment

behavior has been described as “proximity-, comfort- or security-seeking when facing with some kind of stress”, and particularly secure attachment between a child and a caregiver has been associated with resilience.³ Later in life, warm family support and robust social relationships buffer against adversities.³ Dogs can form close relationships with individuals of the same and different species.⁵⁷ Many dogs are living in single-dog households, and the only close relationships they have are with humans. Dog–human attachment has been shown to have many similarities to child–parent attachment⁵⁷ and secure and insecure attachment-types can also be found in dog–human relationships.⁵⁷ Dog–human relationship, human personality and human attachment have been shown to have a large effect on stress coping in dogs.⁵⁸ In the long run, dogs and their owners seem to have similar stress levels, suggesting that the owner and especially the owner's personality and behavior are a major source of resilience in dogs.⁵⁹ Positive interaction with the owner, such as play, may well increase the dog's resilience. Studies have shown that playing with humans reduces blood cortisol levels and reduces stress, both in humans and in dogs.⁶⁰ Play behavior in rats increases plasticity in neurons, which is associated with individual resilience later in life.⁶¹ In dogs, training and engaging in competitions also seem to act as protective agents against the dog's cognitive decline.⁶²

In children, several studies have shown that physical punishment is a risk factor for psychopathology in the children,^{2,63} and thus a risk factor for resilience. Also, in dogs, an association between harsh training methods and the dog's tendency to show fear, attention-seeking and aggression have been found,⁶⁴ however, no causality could be shown. It may be, that aggressive dogs are trained using harsh methods, because these dogs are difficult to handle, or alternatively, aggressiveness is a result of harsh training methods. Research in children has also shown that the children's own coercive and challenging behavior may induce the use of harsh discipline from adults.² A similar observation has also been made on dogs. Belgian Malinois dogs, dopamine transporter polymorphism (genotype 1/1), is associated with high activity, sudden aggressiveness and restlessness, and these dogs are thus difficult to handle.⁶⁵ These dogs are trained by their handlers using more punishment compared to dogs not having this genotype,⁶⁵ suggesting that the dogs' “difficult” behavior provokes handlers to use more coercive training methods. Most likely both types of causalities underlie the observed association between behavioral problems and coercive training methods.

Dogs can also form close relationships with other dogs, and with other pets in the household. Although detailed studies

on dog–dog relationships and their type are largely lacking, few studies indicate that the presence of other (familiar) dogs in the home may support resilience.^{39,66,67} Dogs coming from multi-dog households have been observed to have less fears and aggression compared with dogs from households with only one dog.^{39,66} Moreover, the company of other dogs has been associated with faster recovery from a fearful experience (simulated thunderstorm).⁶⁷ Noise phobic dogs living with conspecifics were observed to have less pronounced reactivity and faster recovery (HPA response) from the fearful stimuli, compared with noise phobic dogs from single-dog households.⁶⁷ Wolves and wild dogs have complex social structures, and only rarely live alone. Therefore, it is hardly surprising, that the company of other dogs may work as stress resilience.³⁹ However, the amount of resilience most likely depends highly on the mutual relationships between dogs in multi-dog households. In rodents, it is well known, that social stress can have long-lasting adverse effects.³ The social defeat paradigm is a test battery, where juvenile mice are predisposed to severe social stress.³ Mice at the age of 6–10 weeks (age that corresponds adolescence in humans) are placed into the same cage together with a more aggressive and larger mouse for 10 mins.³ After this, the young mice are placed into a nearby cage, where these young mice still see the larger and aggressive mice but are no longer in physical contact.³ This procedure is then repeated for 10 days. Social defeat experiment has been observed to result in high corticosterone levels, anxiety-like behavior, and several cellular and molecular changes.³ In multi-dog households, growing up in an unstable, aggressive and hostile environment can have serious negative effects on resilience. If no clear dominance hierarchy exists, dogs may end up in repeated aggressive interactions. Sometimes even in the presence of clear hierarchy, it may be that the most subordinate individuals get bullied, with no chance to escape or leave the household.

Exercise

High physical activity in humans is consistently linked to good mental health outcomes.⁶⁸ Also, in rodents, the high level of physical activity is associated with enhanced neuroplasticity and an improved stress response, and it seems to alleviate the effects of psychological stressors.³ By enhancing neuroplasticity, exercise may promote the individual's capacity for behavioral adaptation across situations.⁶⁹ Physical exercise has also been shown to alleviate the outcomes in certain neurological diseases in humans (depression, Alzheimer's disease, Parkinson's disease, epilepsy, stroke).⁷⁰

In dogs, the daily amount of exercise has been found to be associated with various anxieties. Dogs that did not have 1) noise sensitivity, 2) separation anxiety or 3) fearfulness exercised significantly more compared with dogs having these anxieties.³⁹ Less fearful dogs have also been found to take longer walks.⁷¹ Large study in Labradors found that dogs that had higher levels of daily exercise, were less aggressive and had less fearfulness and separation anxiety compared to dogs that exercised less.⁷² This and other studies suggest that high level of exercise is beneficial also for the dog's mental health.⁷² Nevertheless, no causality is yet shown in dogs, i.e. it is not clear where the effect originates. These correlations may also be explained by the fact that fearful and noise phobic dogs are taken for shorter walks, because they are afraid of the surroundings. However, one study clearly supports the explanation that exercise ameliorates anxiety. A correlation was found between the amount of exercise and the age of onset of noise fear, in a population (N =113), where all dogs had noise fear – dogs having more exercise, and especially free-running, had significantly later onset of noise fear.³⁹

Genetic Factors

Genetic differences may also explain why people and animals respond to and behave differently in the same environment. Genes involved in the HPA axis regulation, such as glucocorticoid receptor (*GR*) and *FKBP5* are associated with individual resilience.⁵ In addition, serotonin transporter genes, *COMT*, *BDNF* and gene coding for neuropeptide Y (*NPY*) have been found to be associated with resilience in rodent and human studies.⁵ Some early research revealed simple gene–environment interactions (GxE), which means that either having a certain allele or exposure to an environmental stressor does not alone result in the outcome, but instead both are needed for the outcome. For example, certain alleles of the genes *5HTT*, *FKBP5* and *CRH1* together with stressful life events were found to increase the risk for psychiatric illness.^{5,73} Some studies report heritability values for the resilience-trait (approximately 30%)⁷⁴ however most genetic studies have investigated the genetics/heritability of either personality traits or psychiatric disorders. Heritability of human personality has been observed to vary (depending on the questionnaire used in the assessment) between 17% and 65% (reviewed in Sanchez-Roige⁷⁵). Many psychiatric disorders have also a very high heritability, nevertheless the genetic mapping of the associated genetic loci has not been easy.⁷⁶ Often, several environmental and multiple

genetic factors affect the human personality traits,⁷⁵ as well as the risk of psychiatric illness in humans⁷⁶ and one single gene usually has a very small effect. A good example is the genetics of depression, which also seems to be highly polygenic.⁷⁷ To date, 102 genetic loci has been found to associate with depression, but it has been estimated that even thousands of loci each having small effects could be linked to depression (reviewed in McIntosh et al⁷⁷). Similarly, a recent meta-analysis identified 136 genomic loci that were associated with neuroticism personality.⁷⁸ In general, genetics behind psychiatric disorders include both small-effect-size common variants and large-effect-size rare variants.⁷⁶

In dogs, several genetic loci were found to have either increased risk or protective effect for fearfulness and aggressiveness towards unfamiliar humans or dogs,³¹ and in addition, different loci for aggressiveness towards family members.³¹ This study found that the allele having protective effect against fearfulness and aggressiveness was common in most of the studied dog breeds (N = 30), except for the two breeds, Dachshunds and Yorkshire Terriers, that carried the risk allele.³¹ The same study also found that *IGF1* and *HMGA2* loci variants that are associated with small body size in dogs, were also associated with several anxiety related behaviors.³¹ Thus, this study suggests that some small-sized dogs may have increased fearfulness,³¹ and maybe lower resilience due to the genetic factors. These loci are not, however, the only genetic factors affecting anxiety and aggression in dogs. A recent study found a genomic area in German Shepherds, that differed between dogs having noise fear and those without noise fear.⁷⁹ The same study identified genetic differences (from another chromosome) between fearful and non-fearful dogs.⁷⁹ In addition, a study focusing on breed differences in behavioral traits observed very high heritabilities (h^2 : 0.27–0.77) for 14 behavioral traits such as aggression and fear towards strangers, trainability, and non-social social fear, and moreover, found 131 single nucleotide polymorphism associated with behavior.⁸⁰ All in all, this suggests that in dogs there is a genetic predisposition to several behavioral and personality traits such as fearfulness and noise fear, however, it also means that dogs may have protective alleles against developing general fearfulness or noise fears.

Findings from these genetic studies suggest that we can increase dogs' resilience by breeding. Do we favor resilience in dog breeding? A study that investigated two Australian Kelpie populations, working kelpies and a pet population of kelpies, suggests that breeding for resilience may happen in certain, but not in all, populations.⁸¹ They found a selective

sweep in the working dog population, and genes in this area were associated with fear-memory formation and pain perception.⁸¹ The selective sweep was found only in active working stock dogs, but was not observed in the pet population, which is bred mainly for conformation.⁸¹ This study suggests that active working stock was bred for traits such as pain perception and fear-memory formation – traits supporting resilience.⁸¹ In a pet population, this was not observed, and the breeding in this population is most likely more focused on conformation and coat color, as it happens to be in most breeds.⁸¹ Although this probably needs further investigation, also Svartberg (2005) found evidence that breed's recent selection (and not the past historical selection) was associated with personality traits that are important for resilience (N > 13 000 dogs).²⁷ Selection for dog shows (breeding for conformation), was associated with increased social and non-social fearfulness, and negatively associated with aggressiveness, playfulness and curiosity.²⁷ Instead, working trial merits were positively correlated with playfulness and aggressiveness.²⁷

Epigenetics

Early experiences often have a profound impact on individuals' functioning across their life span; however, the effect of these experiences does not necessary end there but continues across several generations. Epigenetics refers to heritable modifications of gene expression, without any change to the DNA sequence.³⁸ Several animal and human studies show that adverse environmental effects (for example trauma, maternal separation, unpredictable maternal stress) can cause long-term modifications of stress susceptibility, which can be detected after several generations.^{38,82,83} It has also been suggested that positive experiences may lead to epigenetic changes that are crucial for successful learning and stress management.⁸⁴ An enriched early growing environment has large beneficial effects for animals.^{44,45} It is often assumed that the beneficial effects of an enriched environment are the result of an animal itself experiencing the enriched environment. However, studies have suggested that the beneficial effects of enriched environment (complex housing) can be mediated via epigenetic effects across generations.⁴⁴ This highlights the value of positive experiences, as they affect not only at the individual level, but possibly also across generations.⁴⁴

Microbiota And Diet

The human and animal gut microbiota includes various microorganisms such as bacteria, yeasts, archaea, eukaryotes, and

viruses.⁸⁵ The complexity and diversity of the gut microbiota have a close relationship with health and stress resistance (reviewed in Rea et al 2015⁸⁵). Studies in mice and humans suggest that gut microbiota influences various social, emotional and anxiety-like behaviors.^{44,85} In humans, infants are exposed to mother's microbes during and shortly after the birth.⁸⁵ Infant's gut microbiota is influenced by the type of the delivery (C-section or vaginally born) and whether the baby is breast- or bottle-fed.⁸⁵ As in humans, dogs may also give birth via C-section, and some dog puppies, as human babies, are also bottle-fed, and these most likely influence the microbiota. Individual's neural development is affected by those microbes that populate the gut in early life.⁸⁵ At these critical periods, many environmental factors such as stress or antibiotics may have long-lasting effects on gut-brain signaling, health and these factors may even increase the risk for neurodevelopmental disorders.⁸⁵ Human and canine gut's functional capacity and fecal microbial phylogeny are similar.⁸⁶ In addition, dogs also share microbiota with their human family.⁸⁷ Even though more detailed canine studies are still lacking, it may be safe to speculate that the factors found to be associated with microbiota in humans and rodents, are most likely important also in dogs.

Dietary interventions may also increase stress resilience in animals.⁴⁴ Several laboratory rodent studies, but only few human studies show benefits of prebiotic or probiotic dietary supplements on stress behavior.⁸⁵ Diet which is restricted in calories has been shown to have many beneficial effects, including protection against depressive-like behavior and stress in rodents.³ Dietary tryptophan, which is a precursor of serotonin, has been reported to enhance the recovery from stress in pigs.⁸⁸ Although some associations have been found between tryptophan and anxiety in dogs,⁸⁹ mixed results are however found on the ameliorating effect on canine behavioral problems,^{90,91} and on anxiety and depression in rodents.⁹² More research is needed to find out both the optimal and the safe level of intake, as well as possible consequences on the problem behavior.⁹³ Vitamins and minerals are important for normal brain functioning in humans and in animals.⁹⁴ Dogs that received dietary supplements, especially vitamin B6 and C, expressed less tail chasing (one form of stereotypic behavior) compared to dogs that did not get any dietary supplements.²⁰ This is, however, a purely correlational observation, and needs more investigation. Dietary supplements have also been shown to improve cognition or delay cognitive decline due to aging in dogs in the laboratory; however, evidence is missing from the pet dogs.⁹⁵ Research on the effects of diet is challenging, and

more studies are needed to verify the potential effects of diet on the stress and resilience of individuals.

Conclusions And Future Research

It seems that as in humans, resilience in dogs is a complex mixture of genetic and environmental factors. There exists already some evidence on several key factors supporting resilience in dogs, where factors in early life such as good maternal care, environmental enrichments and socialization (including adoption age and several positive experiences from the environment) are among the most important ones. Some evidence also exists that bold and social personality may buffer against adversities also in dogs. As personalities differ between breeds and between different sized dogs, it may well be that some breeds are more resistant to stress than others. Breeding for stress resilience (favoring personality traits associated with resilience in breeding) should be one of the major goals of breeding in every dog breed; however, the major criteria around the world still are the appearance. There is also some evidence that owner personality, secure attachment and positive interaction with the dog (play, exercise, training, diet) are important environmental factors supporting resilience. In the future, detailed studies in dogs investigating the possible effects of various factors such as personality, breed, maternal care, exercise and microbiota, on individual recovery after adversity might further increase our understanding of the complex interplay between environment and genetics affecting resilience.

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References

1. Scheffer M, Bolhuis J, Borsboom D, et al. Quantifying resilience of humans and other animals. *Proc Natl Acad Sci U S A*. 2018;115(47):11883–11890. doi:10.1073/pnas.1810630115
2. Rutter M. Implications of resilience concepts for scientific understanding. *Ann N Y Acad Sci*. 2006;1094:1–12. doi:10.1196/annals.1376.002
3. Rutten BPF, Hammels C, Geschwind N, et al. Resilience in mental health: linking psychological and neurobiological perspectives. *Acta Psychiatr Scand*. 2013;128(1):3–20. doi:10.1111/acps.12095
4. Rooney NJ, Clark CCA, Casey RA. Minimizing fear and anxiety in working dogs: a review. *J Vet Behav*. 2016;16(C):53–64. doi:10.1016/j.jveb.2016.11.001

5. Feder A, Nestler EJ, Charney DS. Psychobiology and molecular genetics of resilience. *Nat Rev Neurosci.* 2009;10(6):446. doi:10.1038/nrn2649
6. Russo SJ, Murrough JW, Han M, Charney DS, Nestler EJ. Neurobiology of resilience. *Nat Neurosci.* 2012;15(11):1475. doi:10.1038/nn.3234
7. Liu H, Zhang C, Ji Y, Yang L. Biological and psychological perspectives of resilience: is it possible to improve stress resistance? *Front Hum Neurosci.* 2018;12. doi:10.3389/fnhum.2018.00326
8. McEwen BS, Gray JD, Nasca C. Recognizing resilience: learning from the effects of stress on the brain. *Neurobiol Stress.* 2015;1(C):1–11. doi:10.1016/j.yinstr.2014.09.001
9. Thompson ER. Development and validation of an international English big-five mini-markers. *Pers Individ Dif.* 2008;45(6):542–548. doi:10.1016/j.paid.2008.06.013
10. Oshio A, Taku K, Hirano M, Saeed G. Resilience and Big Five personality traits: a meta-analysis. *Pers Individ Dif.* 2018;127:54–60. doi:10.1016/j.paid.2018.01.048
11. Sarubin N, Wolf M, Giegling I, et al. Neuroticism and extraversion as mediators between positive/negative life events and resilience. *Pers Individ Dif.* 2015;82:193–198. doi:10.1016/j.paid.2015.03.028
12. Svartberg K, Forkman B. Personality traits in the domestic dog (*Canis familiaris*). *Appl Anim Behav Sci.* 2002;79(2):133–155. doi:10.1016/S0168-1591(02)00121-1
13. Jones AC, Gosling SD. Temperament and personality in dogs (*Canis familiaris*): a review and evaluation of past research. *Appl Anim Behav Sci.* 2005;95(1–2):1–53. doi:10.1016/j.applanim.2005.04.008
14. Ley JM, Bennett PC, Coleman GJ. Personality dimensions that emerge in companion canines. *Appl Anim Behav Sci.* 2008;110(3):305–317. doi:10.1016/j.applanim.2007.04.016
15. Ley JM, Bennett PC, Coleman GJ. A refinement and validation of the Monash Canine Personality Questionnaire (MCPQ). *Appl Anim Behav Sci.* 2009;116(2):220–227. doi:10.1016/j.applanim.2008.09.009
16. Bateson M, Brilot B, Nettle D. Anxiety: an evolutionary approach. *Can J Psychiatry.* 2011;56(12):707–715. doi:10.1177/070674371105601202
17. Siniscalchi M, McFarlane JR, Kauter KG, Quaranta A, Rogers LJ. Cortisol levels in hair reflect behavioural reactivity of dogs to acoustic stimuli. *Res Vet Sci.* 2013;94(1):49–54. doi:10.1016/j.rvsc.2012.02.017
18. Overall KL, Dunham AE, Frank D. Frequency of nonspecific clinical signs in dogs with separation anxiety, thunderstorm phobia, and noise phobia, alone or in combination. *J Am Vet Med Assoc.* 2001;219(4):467–473. doi:10.2460/javma.2001.219.467
19. Tiira K, Sulkama S, Lohi H. Prevalence, comorbidity, and behavioral variation in canine anxiety. *J Vet Behav.* 2016;16:36–44. doi:10.1016/j.jveb.2016.06.008
20. Tiira K, Hakosalo O, Kareinen L, et al. Environmental effects on compulsive tail chasing in dogs. *PLoS One.* 2012;7(7):e41684. doi:10.1371/journal.pone.0041684
21. Werner EE. Resilient children. *Young Child.* 1984;40(1):68–72.
22. Zolkoski SM, Bullock LM. Resilience in children and youth: a review. *Child Youth Serv Rev.* 2012;34(12):2295–2303. doi:10.1016/j.childyouth.2012.08.009
23. Riemer S, Mills D, Wright H. Impulsive for life? The nature of long-term impulsivity in domestic dogs. *Anim Cogn.* 2014;17(3):815–819. doi:10.1007/s10071-013-0701-4
24. Wright HF, Mills DS, Pollux PMJ. Behavioural and physiological correlates of impulsivity in the domestic dog (*Canis familiaris*). *Physiol Behav.* 2012;105(3):676–682. doi:10.1016/j.physbeh.2011.09.019
25. Wormald D, Lawrence AJ, Carter G, Fisher AD. Reduced heart rate variability in pet dogs affected by anxiety-related behaviour problems. *Physiol Behav.* 2017;168:122–127. doi:10.1016/j.physbeh.2016.11.003
26. Corsetti S, Borruso S, Di Traglia M, et al. Bold personality makes domestic dogs entering a shelter less vulnerable to diseases. *PLoS One.* 2018;13(3):e0193794. doi:10.1371/journal.pone.0193794
27. Svartberg K. Breed-typical behaviour in dogs—historical remnants or recent constructs? *Appl Anim Behav Sci.* 2006;96(3):293–313. doi:10.1016/j.applanim.2005.06.014
28. Turcsán B, Miklósi Á, Kubinyi E. Owner perceived differences between mixed-breed and purebred dogs. *PLoS One.* 2017;12(2):e0172720. doi:10.1371/journal.pone.0172720
29. Turcsán B, Kubinyi E, Miklósi Á. Trainability and boldness traits differ between dog breed clusters based on conventional breed categories and genetic relatedness. *Appl Anim Behav Sci.* 2011;132(1):61–70. doi:10.1016/j.applanim.2011.03.006
30. McGreevy P, Georgevsky D, Carrasco J, et al. Dog behavior covaries with height, bodyweight and skull shape. *PLoS One.* 2013;8(12):e80529. doi:10.1371/journal.pone.0080529
31. Zapata I, Serpell JA, Alvarez CE. Genetic mapping of canine fear and aggression. *BMC Genomics.* 2016;17(1):572. doi:10.1186/s12864-016-3328-4
32. Segovia F, Moore JL, Linnville SE, Hoyt RE, Hain RE. Optimism Predicts Resilience in Repatriated Prisoners of War: A 37-Year Longitudinal Study. *J Trauma Stress.* 2012;25(3):330–336. doi:10.1002/jts.21691
33. Karagiannis C, Burman O, Mills D. Dogs with separation-related problems show a “less pessimistic” cognitive bias during treatment with fluoxetine (Reconcile™) and a behaviour modification plan. *BMC Vet Res.* 2015;11:1. doi:10.1186/s12917-015-0373-1
34. Cockburn A, Smith M, Rusbridge C, et al. Evidence of negative affective state in Cavalier King Charles Spaniels with syringomyelia. *Appl Anim Behav Sci.* 2018;201:77–84. doi:10.1016/j.applanim.2017.12.008
35. Wells DL, Hepper PG, Milligan ADS, Barnard S. Cognitive bias and paw preference in the domestic dog (*Canis familiaris*). *J Comp Psychol.* 2017;131(4):317–325. doi:10.1037/com0000080
36. Barnard S, Wells DL, Milligan ADS, Amott G, Hepper PG. Personality traits affecting judgement bias task performance in dogs (*Canis familiaris*). *Sci Rep.* 2018;8(1):6660. doi:10.1038/s41598-018-25224-y
37. Rusting CL. Interactive effects of personality and mood on emotion-congruent memory and judgment. *J Pers Soc Psychol.* 1999;77(5):1073–1086. doi:10.1037/0022-3514.77.5.1073
38. Meaney MJ. Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annu Rev Neurosci.* 2001;24(1):1161–1192. doi:10.1146/annurev.neuro.24.1.1161
39. Tiira K, Lohi H. Early life experiences and exercise associate with canine anxieties. *PLoS One.* 2015;10(11):e0141907. doi:10.1371/journal.pone.0141907
40. Guardini G, Mariti C, Bowen J, et al. Influence of morning maternal care on the behavioural responses of 8-week-old beagle puppies to new environmental and social stimuli. *Appl Anim Behav Sci.* 2016;181:137–144. doi:10.1016/j.applanim.2016.05.006
41. Foyer P, Wilsson E, Jensen P. Levels of maternal care in dogs affect adult offspring temperament. *Sci Rep.* 2016;6(1):19253. doi:10.1038/srep19253
42. Leckman JF, Herman AE. Maternal behavior and developmental psychopathology. *Biol Psychiatry.* 2002;51(1):27–43. doi:10.1016/S0006-3223(01)01277-X
43. Dwyer CM, Gilbert CL, Lawrence AB. Prepartum plasma estradiol and postpartum cortisol, but not oxytocin, are associated with interindividual and breed differences in the expression of maternal behaviour in sheep. *Horm Behav.* 2004;46(5):529–543. doi:10.1016/j.yhbeh.2004.05.011
44. Kolb B, Harker A, Gibb R. Principles of plasticity in the developing brain. *Dev Med Child Neurol.* 2017;59(12):1218–1223. doi:10.1111/dmcn.13546
45. Dudley KJ, Li X, Kobor MS, Kippin TE, Bredy TW. Epigenetic mechanisms mediating vulnerability and resilience to psychiatric disorders. *Neurosci Biobehav Rev.* 2011;35(7):1544–1551. doi:10.1016/j.neubiorev.2010.12.016
46. Vaterlaws-Whiteside H, Hartmann A. Improving puppy behavior using a new standardized socialization program. *Appl Anim Behav Sci.* 2017;197:55–61. doi:10.1016/j.applanim.2017.08.003
47. Pluijmakers JJTM, Appleby DL, Bradshaw JWS. Exposure to video images between 3 and 5 weeks of age decreases neophobia in domestic dogs. *Appl Anim Behav Sci.* 2010;126(1):51–58. doi:10.1016/j.applanim.2010.05.006

48. Jokinen O, Appleby D, Sandbacka-Saxén S, Appleby T, Valros A. Homing age influences the prevalence of aggressive and avoidance-related behaviour in adult dogs. *Appl Anim Behav Sci.* 2017;195(C):87–92. doi:10.1016/j.applanim.2017.06.003
49. Scott JP, Fuller JL. *Genetics and the Social Behavior of the Dog*. Chicago, IL: Univ. of Chicago Press; 1965.
50. Wells DL, Hepper PG. Prevalence of behaviour problems reported by owners of dogs purchased from an animal rescue shelter. *Appl Anim Behav Sci.* 2000;69(1):55–65. doi:10.1016/S0168-1591(00)00118-0
51. Serpell J, Jagoe JA. Early experience and the development of behaviour. In: Serpell J, editor. *The Domestic Dog. Its Evolution, Behaviour and Interactions with People*. Cambridge: Cambridge University Press; 1995:80–102.
52. Coppola CL, Grandin T, Enns RM. Human interaction and cortisol: can human contact reduce stress for shelter dogs? *Physiol Behav.* 2006;87(3):537–541. doi:10.1016/j.physbeh.2005.12.001
53. Wallis LJ, Szabo D, Erdelyi-Belle B, Kubinyi E. Demographic change across the lifespan of pet dogs and their impact on health status. *Front Vet Sci.* 2018;5. doi:10.3389/fvets.2018.00040
54. Rutter M. Resilience as a dynamic concept. *Dev Psychopathol.* 2012;24(2):335–344. doi:10.1017/S0954579412000028
55. Levine S, Mody T. The long-term psychobiological consequences of intermittent postnatal separation in the squirrel monkey. *Neurosci Biobehav Rev.* 2003;27(1):83–89. doi:10.1016/S0149-7634(03)00011-3
56. Gazzano A, Mariti C, Notari L, Sighieri C, McBride EA. Effects of early gentling and early environment on emotional development of puppies. *Appl Anim Behav Sci.* 2008;110(3):294–304. doi:10.1016/j.applanim.2007.05.007
57. Payne E, Bennett PC, McGreevy PD. Current perspectives on attachment and bonding in the dog-human dyad. *Psychol Res Behav Manage.* 2015;8:71–79. doi:10.2147/PRBM.S74972
58. Schoberl I, Wedl M, Bauer B, Day J, Mostl E, Kotschal K. Effects of owner-dog relationship and owner personality on cortisol modulation in human-dog dyads. *Anthrozoos.* 2012;25(2):199–214. doi:10.2752/175303712X13316289505422
59. Sundman A, Van Poucke E, Svensson Holm A, et al. Long-term stress levels are synchronized in dogs and their owners. *Sci Rep.* 2019;9(1). doi:10.1038/s41598-019-43851-x
60. Roth LSV, Faresjö Å, Theodorsson E, Jensen P. Hair cortisol varies with season and lifestyle and relates to human interactions in German shepherd dogs. *Sci Rep.* 2016;6(1). doi:10.1038/srep19631
61. Bell HC, Pellis SM, Kolb B. Juvenile peer play experience and the development of the orbitofrontal and medial prefrontal cortices. *Behav Brain Res.* 2010;207(1):7–13. doi:10.1016/j.bbr.2009.09.029
62. Szabó D, Miklósi Á, Kubinyi E. Owner reported sensory impairments affect behavioural signs associated with cognitive decline in dogs. *Behav Processes.* 2018;157:354–360. doi:10.1016/j.beproc.2018.07.013
63. Jones, DPH. Child maltreatment. In: Rutter M, Bishop D, Pine D editors. *Rutter's Child and Adolescent Psychiatry*. Singapore: Blackwell Publishing, Limited; 2008:421–439.
64. Blackwell EJ, Twells C, Seawright A, Casey RA. The relationship between training methods and the occurrence of behavior problems, as reported by owners, in a population of domestic dogs. *J Vet Behav.* 2008;3(5):207–217. doi:10.1016/j.jvbeh.2007.10.008
65. Lit L, Belanger JM, Boehm D, et al. Characterization of a dopamine transporter polymorphism and behavior in Belgian Malinois. *BMC Genet.* 2013;14(45):45. doi:10.1186/1471-2156-14-33
66. Serpell JA, Duffy DL. Aspects of juvenile and adolescent environment predict aggression and fear in 12-month-old guide dogs. *Front Vet Sci.* 2016;3(June):49. doi:10.3389/fvets.2016.00049
67. Dreschel NA, Granger DA. Physiological and behavioral reactivity to stress in thunderstorm-phobic dogs and their caregivers. *Appl Anim Behav Sci.* 2005;95(3):153–168. doi:10.1016/j.applanim.2005.04.009
68. Salmon P. Effects of physical exercise on anxiety, depression, and sensitivity to stress: a unifying theory. *Clin Psychol Rev.* 2001;21(1):33–61. doi:10.1016/S0272-7358(99)00032-X
69. Hötting K, Röder B. Beneficial effects of physical exercise on neuroplasticity and cognition. *Neurosci Biobehav Rev.* 2013;37(9):2243–2257. doi:10.1016/j.neubiorev.2013.04.005
70. Wrann CD, White JP, Salogiannnis J, et al. Exercise Induces Hippocampal BDNF through a PGC-1 α /FNDC5 Pathway. *Cell Metab.* 2013;18(5):649–659. doi:10.1016/j.cmet.2013.09.008
71. Tami G, Barone A, Diverio S. Relationship between management factors and dog behavior in a sample of Argentine Dogs in Italy. *J Vet Behav.* 2008;3(2):59–73. doi:10.1016/j.jvbeh.2007.09.002
72. Lofgren SE, Wiener P, Blott SC, et al. Management and personality in Labrador Retriever dogs. *Appl Anim Behav Sci.* 2014;156:44–53. doi:10.1016/j.applanim.2014.04.006
73. Elbau IG, Cruceanu C, Binder EB. Genetics of resilience: gene-by-environment interaction studies as a tool to dissect mechanisms of resilience (Report). *Biol Psychiatry.* 2019;86(6):433. doi:10.1016/j.biopsych.2019.04.025
74. Amstadter AB, Myers JM, Kendler KS. Psychiatric resilience: longitudinal twin study. *Br J Psychiatry.* 2014;205(4):275. doi:10.1192/bjp.bp.113.130906
75. Sanchez-Roige S, Gray JC, Mackillop J, Chen C, Palmer AA. The genetics of human personality. *Genes Brain Behav.* 2018;17(3):e12439. doi:10.1111/gbb.2018.17.issue-3
76. Geschwind DH, Flint J. Genetics and genomics of psychiatric disease. *Science.* 2015;349(6255):1489. doi:10.1126/science.aaa8954
77. McIntosh AM, Sullivan PJ, Lewis CM. Uncovering the genetic architecture of major depression. *Neuron.* 2019;102(1):91–103. doi:10.1016/j.neuron.2019.03.022
78. Nagel M, Jansen PR, Stringer S, et al. Meta-analysis of genome-wide association studies for neuroticism in 449,484 individuals identifies novel genetic loci and pathways. *Nat Genet.* 2018;50(7):920. doi:10.1038/s41588-018-0151-7
79. Sarviaho R, Hakosalo O, Tiira K, et al. Two novel genomic regions associated with fearfulness in dogs overlap human neuropsychiatric loci. *Transl Psychiatry.* 2019;9:1–11. doi:10.1038/s41398-018-0355-8
80. MacLean EL, Snyder-Mackler N, vonHoldt BM, Serpell JA. Highly heritable and functionally relevant breed differences in dog behaviour. *Proc R Soc B.* 2019;286:20190716. doi:10.1098/rspb.2019.0716
81. Arnott ER, Peek L, Early JB, et al. Strong selection for behavioural resilience in Australian stock working dogs identified by selective sweep analysis. *Canine Genet Epidemiol.* 2015;2(1):6. doi:10.1186/s40575-015-0017-6
82. Jensen P. Behaviour epigenetics - The connection between environment, stress and welfare. *Appl Anim Behav Sci.* 2014;157:1–7. doi:10.1016/j.applanim.2014.02.009
83. Yehuda R, Daskalakis NP, Bierer LM, et al. Holocaust exposure induced intergenerational effects on FKBP5 methylation. *Biol Psychiatry.* 2016;80(5):372–380. doi:10.1016/j.biopsych.2015.08.005
84. Hoffmann A, Spengler D. DNA memories of early social life. *Neuroscience.* 2014;264:64–75. doi:10.1016/j.neuroscience.2012.04.003
85. Rea K, Dinan TG, Cryan JF. The microbiome: a key regulator of stress and neuroinflammation. *Neurobiol Stress.* 2016;4(C):23–33. doi:10.1016/j.ynstr.2016.03.001
86. Deng P. Gut microbiota of humans, dogs and cats: current knowledge and future opportunities and challenges. *Br J Nutr.* 2015;113(S1):S17. doi:10.1017/S0007114514002943
87. Song SJ, Lauber C, Costello EK, et al. Cohabiting family members share microbiota with one another and with their dogs. *eLife.* 2013;12(2):e00458. doi:10.7554/eLife.00458
88. Koopmans SJ, Guzik AC, Van Der Meulen J, et al. Effects of supplemental L-tryptophan on serotonin, cortisol, intestinal integrity, and behavior in weanling piglets. *J Anim Sci.* 2006;84(4):963. doi:10.2527/2006.844963x

89. Puurunen J, Tiira K, Lehtonen M, Hanhineva K, Lohi H. Non-targeted metabolite profiling reveals changes in oxidative stress, tryptophan and lipid metabolisms in fearful dogs. *Behav Brain Funct.* 2016;12(1):7. doi:10.1186/s12993-016-0091-2
90. Denapoli JS, Dodman NH, Shuster L, Rand WM, Gross KL. Effect of dietary protein content and tryptophan supplementation on dominance aggression, territorial aggression, and hyperactivity in dogs. *J Am Vet Med Assoc.* 2000;217(4):504. doi:10.2460/javma.2000.217.504
91. Templeman JR, Davenport GM, Cant JP, Osborne VR, Shoveller A. The effect of graded concentrations of dietary tryptophan on canine behavior in response to the approach of a familiar or unfamiliar individual. *Can J Vet Res.* 2018;82(4):294.
92. Hansen F, de Oliveira DL, Amaral FUÍ, et al. Effects of chronic administration of tryptophan with or without concomitant fluoxetine in depression-related and anxiety-like behaviors on adult rat. *Neurosci Lett.* 2011;499(2):59–63. doi:10.1016/j.neulet.2011.05.032
93. Bosch G, Beerda B, Hendriks WH, Van Der Poel AFB, Verstegen MWA. Impact of nutrition on canine behaviour: current status and possible mechanisms. *Nutr Res Rev.* 2007;20(2):180–194. doi:10.1017/S095442240781331X
94. Bourre J. Effects of nutrients (in food) on the structure and function of the nervous system: update on dietary requirements for brain. Part 1: micronutrients. *J Nutr Health Aging.* 2006;10(5):377–385.
95. Chapagain D, Range F, Huber L, Viranyi Z. Cognitive aging in dogs. *Gerontology.* 2018;64(2):165–171. doi:10.1159/000481621

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