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Personality, Parasites, and Survival: Exploring Free-Ranging Dog Puppies (Canis lupus familiaris)

verfasst von | submitted by

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1 Abstract

Background

Animal personality can influence exposure to parasites and survival, yet little is known about such effects during early development in free-ranging dogs (*Canis lupus familiaris*). This study tested whether personality traits predicted ectoparasite burden, body condition, or survival in puppies during their first 12 weeks of life.

Methods

We monitored 14 litters (n = 107 puppies) in Morocco from birth to 12 weeks of age. Behavioral tests at 5 and 8 weeks assessed sociability towards humans (Human Approach test), sociability towards conspecifics (Fake Dog test), and boldness (Novel Object test). Flea and tick counts, body weight, body condition score (BCS), and survival status were recorded at 5, 8, and 12 weeks. Parasite burden was analyzed using negative-binomial mixed models, body condition with linear and ordinal models, and survival with interval-censored accelerated failure time (AFT) models.

Results

Parasite loads were broadly stable across ages and did not consistently predict subsequent weight or BCS. At 8 weeks, higher sociability towards conspecifics was associated with greater parasite burdens (fleas IRR = 1.40, ticks IRR = 1.49), consistent with increased exposure via social play and expanded contacts. Boldness and human directed sociability showed no clear associations. Neither traits nor parasite burden predicted survival from 5-8 or 8-12 weeks.

Conclusions

Personality–ectoparasite associations in free-ranging dog puppies were age-specific and limited to conspecific sociability at 8 weeks. Early ectoparasite burden did not impair short-term growth or survival, highlighting the dominant role of environmental and anthropogenic pressures in shaping early-life outcomes. These findings underscore the need for larger integrative studies that combine behavior, maternal care, cause of death, and animal–human interactions to understand when and how personality matters in free-ranging populations.

2 Zusammenfassung

Hintergrund

Persönlichkeitszüge können Überleben und Parasitenexposition freilebender Tiere maßgeblich beeinflussen, doch über diese Effekte in der frühen Entwicklung von Straßenhunden (*Canis lupus familiaris*) ist wenig bekannt. Diese Studie untersuchte, ob Persönlichkeitsmerkmale das Überleben oder den Befall mit Ektoparasiten und darüber den Ernährungszustand von Welpen in den ersten 12 Lebenswochen vorhersagen.

Methoden

In Marokko wurden 14 Würfe (n = 107 Welpen) bis zur 12. Lebenswoche beobachtet. In der 5. und 8. Lebenswoche wurde ihr Verhalten getestet und drei Persönlichkeitsmerkmale erfasst: Sozialverhalten gegenüber Menschen (Human Approach Test), Sozialverhalten gegenüber Artgenossen (Fake Dog Test) und Mut (Novel Object Test). Gleichzeitig wurden Flöhe und Zecken gezählt, Überleben, Körpergewicht und Body Condition Score (BCS) dokumentiert und mit gemischten Modellen (negative-binomial, linear, ordinal) sowie intervallzensierten AFT-Modellen ausgewertet.

Ergebnisse

Der Parasitenbefall blieb über die Altersstufen hinweg weitgehend stabil und sagte weder Gewicht noch BCS zuverlässig voraus. In der 8. Lebenswoche war ein sozialeres Verhalten gegenüber Artgenossen mit einem stärkeren Parasitenbefall verbunden (Flöhe IRR = 1.40, Zecken IRR = 1.49). Mut und menschenbezogenes Sozialverhalten zeigten keine klaren Zusammenhänge. Weder Persönlichkeitsmerkmale noch Parasitenanzahl sagten das Überleben zwischen der 5.-8. bzw. 8.-12. Lebenswoche vorher.

Schlussfolgerungen

Zusammenhänge zwischen Persönlichkeitsmerkmalen und Parasitenbefall bei freilebenden Hundewelpen waren altersspezifisch und beschränkten sich auf das Sozialverhalten gegenüber Artgenossen in der 8. Lebenswoche, was auf eine erhöhte Parasitenexposition durch soziale Kontakte beim Spiel und bei zunehmenden Erkundungen hindeutet. Der Befall mit Parasiten beeinträchtigte weder das kurzfristige Wachstum noch das Überleben, was die dominierende Rolle von Umwelt- und anthropogenen Einflüssen in der frühen Lebensphase unterstreicht. Die Ergebnisse verdeutlichen die Notwendigkeit größerer integrativer Studien, die Verhalten, maternale Fürsorge, Todesursachen und Mensch-Tier-Interaktionen kombinieren, um zu verstehen, wann und wie die Persönlichkeit freilebender Populationen und Individuen von Bedeutung ist.

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6 List of Abbreviations

AFT .... *Accelerated-failure-time*
AIC .... *Akaike's Information Criterion*
approx .... *approximately*
BCS.......................... *Body condition score*
BORIS .. *Behavioral Observation Research Interactive Software*
CLMM .... *Cumulative-link mixed model*
cm .... *Centimetre*
Dur .... *Duration*
E .... *Experimenter*
E1....... *Experimenter 1 (testing at 5 weeks)*
E2....... *Experimenter 2 (testing at 8 weeks)*
FD .... *Fake Dog (Test)*
Freq... *Frequenz*
HA......................... *Human approach (test)*
IRR........................... *Incidence rare ratios*
kg... *kilograms*
Lat .... *Latency*
LMM............................ *Linear mixed model*
m .... *Metre*
n .... *Sample size*
NB-GLMM .. *Negative-binomial generalized mixed models*
NO .... *Novel Object (Test)*
OR .... *Odds Ratio*
P .... *Puppy*
Paras .... *Parasites*
PCA .... *Principal Component Analysis*
Soc_Con .. *Sociability towards conspecifics*
Soc_Hum .... *Sociability towards humans*
TR... *Time Ratio*

7 Introduction

The study of animal personality has gained significant attention in recent years, with implications spanning ecology, evolution, and human-animal health. Personality traits influence individual behavior and fitness, affecting processes from ecosystem services to evolutionary dynamics (Hunter et al., 2022; Mortelliti, 2022; Dubois & Binning, 2022). For example, Mortelliti (2022) highlights how animal behavior shapes ecosystem service management, such as the homing instincts of salmonid fish or the foraging habits of sea turtles that lead to plastic ingestion. Meanwhile, Dubois and Binning (2022) predict that ecological factors, including predation pressure, food availability, and parasite prevalence, shape the genetic diversity of personality traits within populations.

Research also highlights the role of personality traits in shaping health outcomes and susceptibility to parasitic infections. Social, bold, and exploratory animals often face higher risks of parasitic infestations due to increased interactions with conspecifics and the environment (Hoffmann, 2014; Møller et al., 1993). However, animals have developed strategies to reduce ectoparasitic loads, such as self-grooming (i.e., body care of oneself) and allogrooming (i.e., body care of a conspecific) (Møller et al., 1993; Mooring, 2024). Grooming can significantly reduce parasite burdens; for example Hinkle et al. (1998) found that self-grooming cats (*Felis catus*) could remove up to 17.6% of their flea burden (*Ctenocephalides felis felis*) per day, while Mooring et al. (1996) reported that free-ranging impala (*Aepyceros melampus*) prevented from oral self-grooming carried 20 times more ticks (*Boophilus decoloratus*) than those able to groom. Similarly, boldness can also confer advantages, such as better immunological resilience. For instance, Corsetti et al. (2018) found that bolder domestic dogs (*Canis lupus familiaris*) in shelters exhibited improved immune parameters and were less prone to diseases than shyer ones, while Costa et al. (2020) demonstrated that bolder and more exploratory tamarins (*Leontopithecus chrysomelas*) had higher body mass and overall better health outcomes. Together, these studies suggest that personality traits like boldness and sociability can have complex, context-dependent effects on health and survival.

Free-ranging dogs (*Canis lupus familiaris*) provide a unique opportunity to examine these dynamics, as they face multifaceted challenges from environmental pressures and frequent human interactions that shape their personalities in ways distinct from other wildlife populations (Brehm et al., 2023). Survival rates among free-ranging dog puppies are low, with human influence playing a significant role (Paul et al., 2016). Traits like boldness and sociability towards both humans and conspecifics may offer survival advantages, as these dogs navigate complex relationships with humans, ranging from receiving food to experiencing hostility (Bhattacharjee et al., 2021).

However, free-ranging dogs are frequently infested with ectoparasites such as fleas (Siphonaptera) and ticks (Ixodida), which not only cause discomfort but can also lead to weight loss, impaired growth, and anorexia (Mooring, 2024; Norval et al., 1988). Moreover, ectoparasites serve as vectors for potentially life-threatening diseases, including leishmaniosis, bartonellosis, borreliosis, and rickettsiosis (Day, 2011) and may cause or indicate a weak immune system of the host (Obiegala et al., 2021; Presley, 2011). Many of these pathogens, such as *Bartonella* and *Rickettsia*, are zoonotic, posing risks to both animal and human health. Fleas and ticks transmit diseases such as murine typhus and Mediterranean spotted fever have also been implicated in chronic idiopathic conditions in humans (Day, 2011; Kelly, 2005; Low et al., 2017).

The One Health framework provides a valuable perspective on these issues, emphasizing the interconnectedness of human, animal, and environmental health. Free-ranging dogs act as a bridge between humans and their environment, facilitating the transmission of zoonotic diseases (Young et al., 2011; Gompper, 2014). Given their close proximity to humans, managing the health and behavior of free-ranging dog populations is not only a matter of animal welfare, but also a public health priority.

Understanding the interplay between personality traits, ectoparasitic burden, and health outcomes is critical, as it can inform strategies to reduce zoonotic risks and improve the welfare of free-ranging dog populations. Despite a growing body of research on animal personality, its relationship with parasitic burden and survival in free-ranging dogs remains underexplored. This thesis addresses this gap by investigating how individual personality traits influence ectoparasitic infestations (fleas and ticks) and survival rates in free-ranging dog puppies. We focus on working with puppies rather than adult dogs to exclude potential biases in sexually mature animals. The age of puppies can be estimated far more reliably than that of adult dogs, which improves the standardization of the research. Additionally, because puppies are not yet sexually mature, hormonal influences are minimized. Traits such as territoriality, pregnancy, and maternal or mating behavior have not yet emerged, reducing heterogeneity among individuals but also potentially leading to changes in personality once these factors appear later in development (Fratkin et al., 2013). Importantly, previous research indicates that personality traits observed in young puppies show short-term consistency, with consistency generally increasing with the dogs' age (Barnard et al., 2016; Fratkin et al., 2013; Riemer et al., 2014). The present study therefore focuses on the short-term consistency of traits during early puppyhood.

Firstly, we hypothesize that puppies exhibiting greater sociability towards conspecifics and higher levels of boldness will have a lower ectoparasite burden due to increased allogrooming and social interactions that may help reduce parasite loads. In line with previous studies, we expect that although higher sociability means increased exposure through more frequent contact, this will be mitigated by the effects of allogrooming.

Secondly, we hypothesize that sociability towards both conspecifics and humans, as well as boldness, will be positively associated with survival rates. This may be due to their improved access to resources and social support, as puppies with these traits could be more successful in navigating their environment and securing food, shelter, or human assistance, thus enhancing their overall chances of survival.

8 Material and Methods

8.1 Study Area and Subjects

The study was conducted in the Souss Massa area in Morocco in the North of Agadir (Figure 1) with a free-ranging dog population of approximately 400 dogs that are genetically distinct from breed dogs (Range and Marshall-Pescini, 2022).

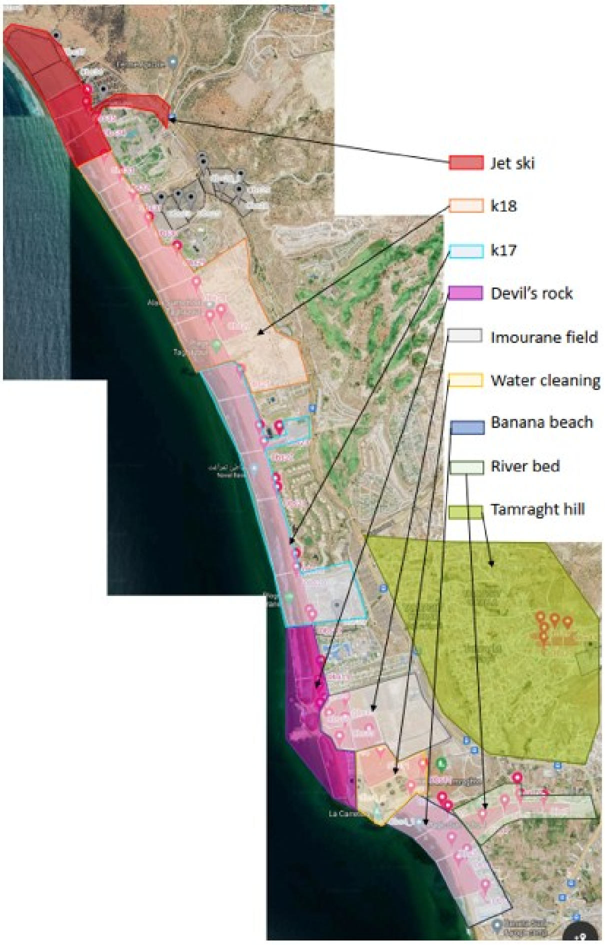

Figure 1. Study area with all observation areas color coded from Aourir to Taghazout and at Tamraght hill.

A cohort of 14 free-ranging dog litters was monitored from birth to 12 weeks (12w) of age. Out of these litters, 8 were assessed for both personality traits and ectoparasites, while 6 litters were assessed for ectoparasites only (Table 1). The litters were identified through systematic monitoring of the free-ranging dog population within the designated observation areas (Figure 1).

Table 1. Number of assessed puppies for personality traits and ectoparasite burden. Litters by female with the number of puppies that were tested and coded at 5 and 8 weeks as well as the number of puppies with parasite assessment done at 5, 8, and 12 weeks. Paras = parasites.

Female dog	Pups tested 5w	Pups tested 8w	Pups paras 5w	Pups paras 8w	Pups paras 12w
Liliane	6	3	6	-	4
Menta	8	5	8	4	-
Lapas	8	-	8	-	-
Irving	4	4	4	4	3
Flav	6	5	6	5	3
Nova	6	5	6	5	3
Beans	9	4	9	4	2
Maria	8	7	8	7	5
Bougainville	-	-	7	7	3
Swill	-	-	4	3	-
Galgos	-	-	7	7	-
Kale	-	-	10	-	10
Juglans	-	-	6	5	2
Styx	-	-	7	3	-
∑	**55**	**33**	**96**	**54**	**35**

As part of ongoing projects at the field site, daily scans were conducted to cover all observation areas. These scans track key events such as females in heat and pregnant females, allowing researchers to estimate when new litters are likely to be born and their potential locations.

The precise den locations and birth dates were further corroborated through reports from local community members. These reports, combined with regular field observations, ensured accurate identification of litters shortly after birth. This systematic approach enabled consistent and detailed observations of the puppies from the earliest stages of life. While survival was continuously monitored, the first physical measurements were conducted when the puppies reached three weeks of age. The same measurements were repeated at 5, 8, and 12 weeks of age, alongside assessments of personality traits and ectoparasite burden. This longitudinal methodology ensured thorough tracking of the puppies' development and health over their early life stages. Only litters that were found in time (not later than approx. 4 weeks of age) were included to be able to estimate the puppies' age reliably.

8.2 Data Collection

8.2.1 Time Period

Data was collected from July to December 2024 for both the personality and the parasite assessments, and continued until April 2025 for the parasite assessment only.

8.2.2 Personality Assessment

Puppies were observed and categorized based on a standardized set of behavioral tests conducted at 5 and 8 weeks of age to investigate how personality traits at these stages related to parasite burden and survival. Traits assessed at 5 weeks were used to investigate parasite burden at the same age and survival up to 8 weeks, while traits assessed at 8 weeks were used to investigate parasite burden at 8 weeks and survival up to 12 weeks. Because personality traits at 8 weeks are considered relatively stable over the following four weeks, they were also used to investigate the associations between personality traits and parasite burden at the 12-week time point (Barnard et al., 2016; Fratkin et al., 2013; MacDonald 1983). The behavioral tests included the Human Approach Test, which measured sociability towards humans (Soc_Hum); the Fake Dog Test, which assessed sociability towards conspecifics (Soc_Con); and the Novel Object Test, which evaluated boldness and reactions to novel stimuli (Capitain et al., 2024).

The tests at 5 and 8 weeks of age were conducted near the litter's den in a controlled environment. The puppies were habituated to the testing setup several days in advance. The testing arena, constructed with portable, opaque fences arranged in a 2 m x 2 m square (Figure 2), was placed near the den, and puppies were given the opportunity to freely explore the structure without any testing procedures taking place. The habituation ensured the puppies were comfortable with the setup and would not react to the testing arena itself as something unfamiliar or stressful during the actual tests.

During the tests, the arena's entry door was closed once the puppy spontaneously entered. The testing process involved two individuals: an experimenter (E) who had no prior interaction with the puppies (one person called E1 at 5 weeks, and a different person called E2 at 8 weeks) and a helper (H) who could be familiar to the puppies. The helper facilitated the tests by managing logistics such as activating cameras, keeping time, and providing cues. They also ensured the area remained distraction-free by handling other dogs (distracting them from the testing arena and keeping them silent, for example with kibble) or curious bystanders nearby. The experimenter, primarily responsible for conducting the tests, interacted directly with the puppy (P) during the tests.

All tests were recorded using two cameras positioned in opposite corners of the fenced area (Figure 2) to capture comprehensive footage of the puppies' behavior.

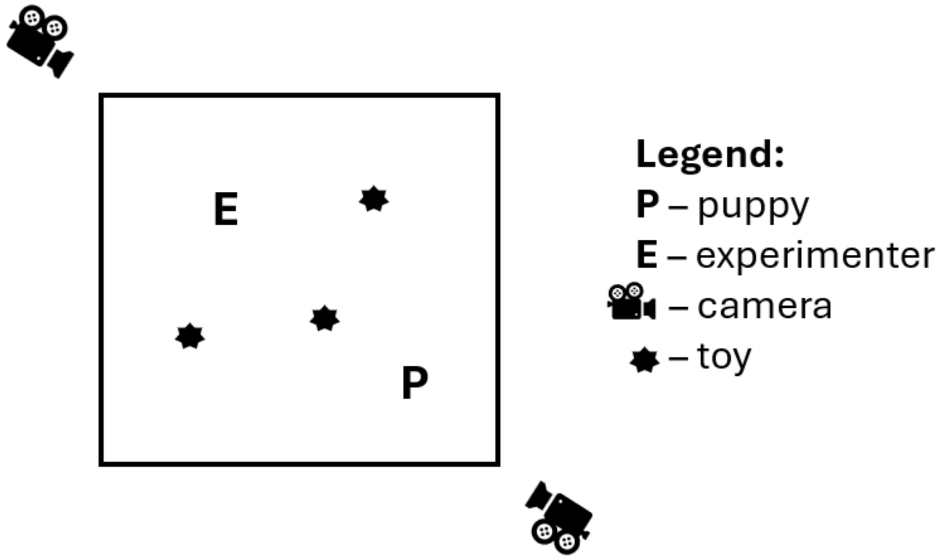

Figure 2. Example of the experimental set-up from Human Approach testing. Testing arena (2 m x 2 m), presenting positions of all the objects. Position of P is based on each individual test subject; other equipment is adjusted based on position of P.

8.2.2.1 Human Approach Test

The Human Approach Test (HA) assesses puppies' reactions to an approaching human, progressing from a neutral interaction to a friendly one. This test aims to evaluate sociability and responses to human interaction in a structured and gradual manner.

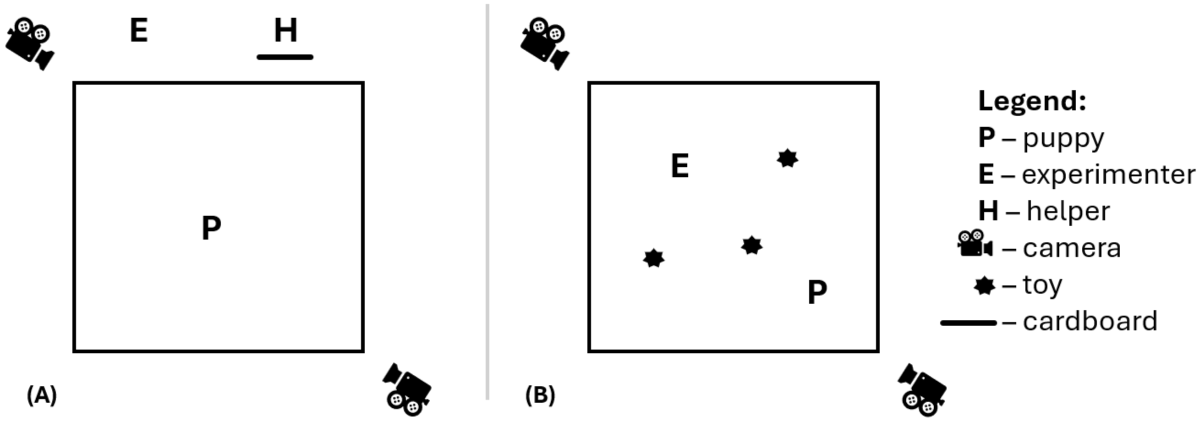

Figure 3. Experimental set-up for Human Approach testing at 5 and 8 weeks of age with (A) the first and second sub-phase "Neutral Approach" and (B) the subsequent phases. Testing arena (2 m x 2 m), presenting positions of all the objects. Position of P is based on each individual test subject; other equipment is adjusted based on position of P.

At 5 and 8 weeks, the test was divided into five sub-phases, each lasting 30 seconds, for a total duration of 2.5 minutes.

1. Neutral Approach: Both the experimenter and the helper approached the testing arena and stood silently outside the fences, maintaining a neutral posture. The helper concealed themselves behind a large cardboard sheet in order to have two stimuli appearing to measure more clearly if the puppy's response is simply to something moving outside of the fences or if it is based on a human stimulus (Figure 3 A).
2. Friendly Speech: The experimenter spoke to the puppy in a friendly tone while remaining outside the arena.
3. Introduction of Toys: Both individuals left the puppy's view. The experimenter then entered the fenced arena and placed three toys – a tennis ball, a rope, and a 15 cm long tug-toy – in the arena. The experimenter sat in one corner, maintaining a neutral facial expression and gaze (Figure 3 B).
4. Friendly Speech: The experimenter began to smile and speak to the puppy in a friendly and engaging manner.
5. Interactive Play: The experimenter picked up the tug-toy and moved it playfully in front of the puppy while smiling and maintaining an inviting demeanor.

This phased approach ensured a gradual escalation from neutral observation to active engagement, allowing the puppy's response to be assessed comprehensively.

8.2.2.2 Fake Dog Test

The Fake Dog Test (FD) is used to simulate interactions with another dog to predict dog-directed sociability. The study of Barnard et al. (2012) indicated that the Fake Dog can reliably evoke behaviors that reflect dogs' responses towards real dogs. The test lasted for 1 minute and was performed without the experimenter being in the fenced area.

A stuffed dog (approx. 50 cm tall) was used as the Fake Dog. It was placed about 50 cm from the puppy, along with 3 toys (the same as in the Human Approach test) (Figure 4). The Fake Dog was positioned in a lateral stance towards the puppy with enough space to go around the Fake Dog. The Fake Dog was covered at all times outside the testing arena to not familiarize the puppies with the Fake Dog before testing, and it was only uncovered for the one minute duration of the experiment. After one minute, the experimenter covered the Fake Dog again and removed it from the testing area.

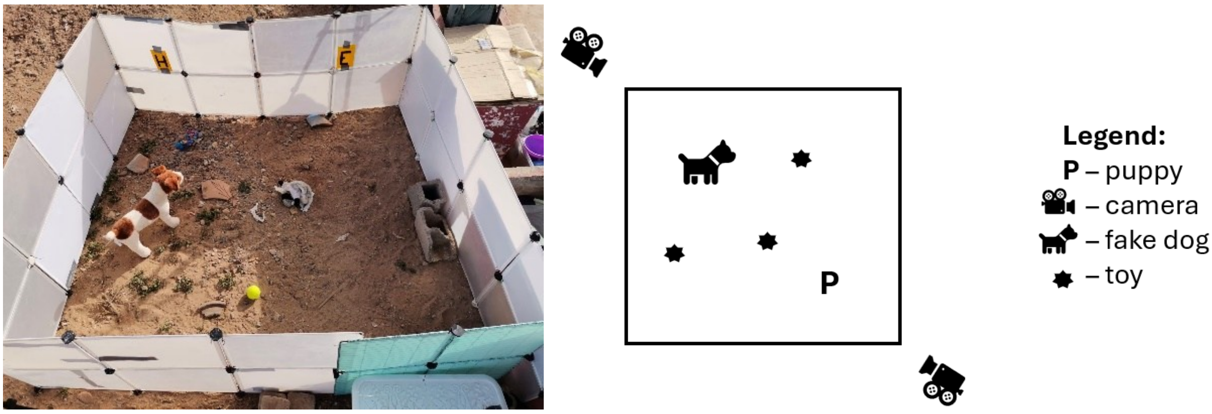

Figure 4. Experimental set-up for Fake Dog testing at 5 and 8 weeks of age. Testing arena (2 m x 2 m), presenting positions of all the objects. Position of P is based on each individual test subject; other equipment is adjusted based on position of P.

8.2.2.3 Novel Object Test

The Novel Object Test (NO) is commonly used to assess boldness by measuring how quickly an animal approaches or interacts with an unfamiliar object. Bolder individuals typically approach novel objects faster and spend more time near them (Barnard et al., 2021).

The Novel Object was a remote-controlled car that was covered until the start of the testing. The experimenter placed the Novel Object on the ground at 50 cm from where the puppy was and surrounded it with 3 toys (a tennis ball, a rope, and a 15 cm long tug-toy; Figure 5). Then the experimenter uncovered the Novel Object and left the arena. The Novel Object Test was divided into two sub-phases, each lasting 30 seconds. In the first sub-phase the car moved around, while it remained still in the second sub-phase.

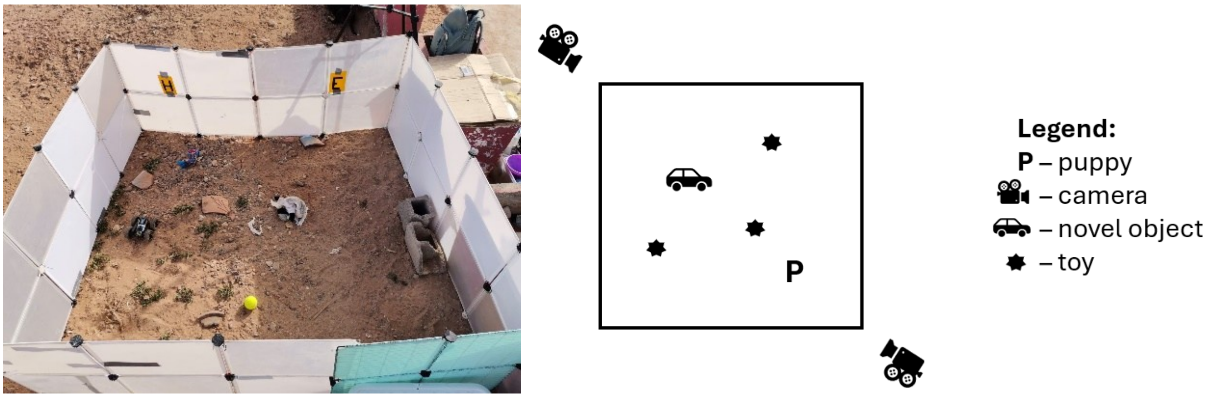

Figure 5. Experimental set-up for Novel Object testing at 5 and 8 weeks of age. Testing arena (2 m x 2 m), presenting positions of all the objects. Position of P is based on each individual test subject; other equipment is adjusted based on position of P.

8.2.3 Ectoparasite Burden

Together with the personality assessment at the age of 5 and 8 weeks, and additionally at 12 weeks the ectoparasite burden was assessed using the flea comb method (Cadiergues et al., 2014; Gregory et al., 1995) and visual inspection. We recorded the presence and abundance of fleas (Siphonaptera) and ticks (Ixodida) but did not identify specimens to species.

For the flea comb method, a fine-toothed comb with 11 teeth per centimetre was used (Marchiondo et al., 2013). The back of the puppy was combed from the neck to the base of the tail for three minutes (in one go or divided into several bouts, depending on the puppy and the number of fleas on the comb), as this area was the most commonly infested body region in dogs (Rinaldi et al., 2007; Figure 6). When the comb became full of fleas or matted with hair, and at least every 30 seconds, fleas and hair were removed by dipping the comb into soapy water. This drowned the fleas and let them sink to the bottom. Right after the combing the fleas were counted in a wide petri dish. (Hinkle et al., 1998).

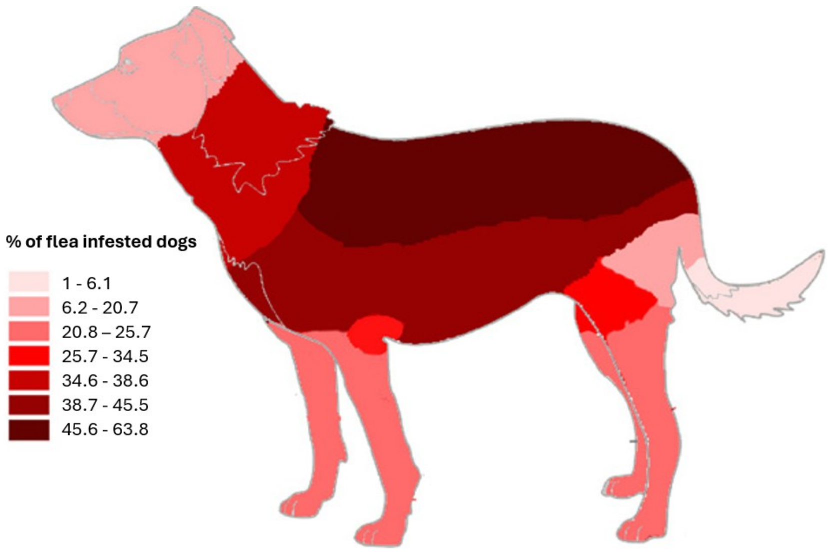

Figure 6. Distribution of fleas across different body parts. Darker red shades indicate higher percentages of flea-infested dogs (up to 63.8%). Puppies were combed along the back, from the neck to the base of the tail. Figure reproduced from Rinaldi et al. (2007), with permission.

Attached ticks were assessed by counting them on the inner side of both the left and right ear of each puppy, extending as deep as the anthelix (Figure 7), as suggested by Marchiondo et al. (2013). The chosen area was independent of fur color and structure, and ticks were clearly visible, making counting both reliable and feasible under field conditions.

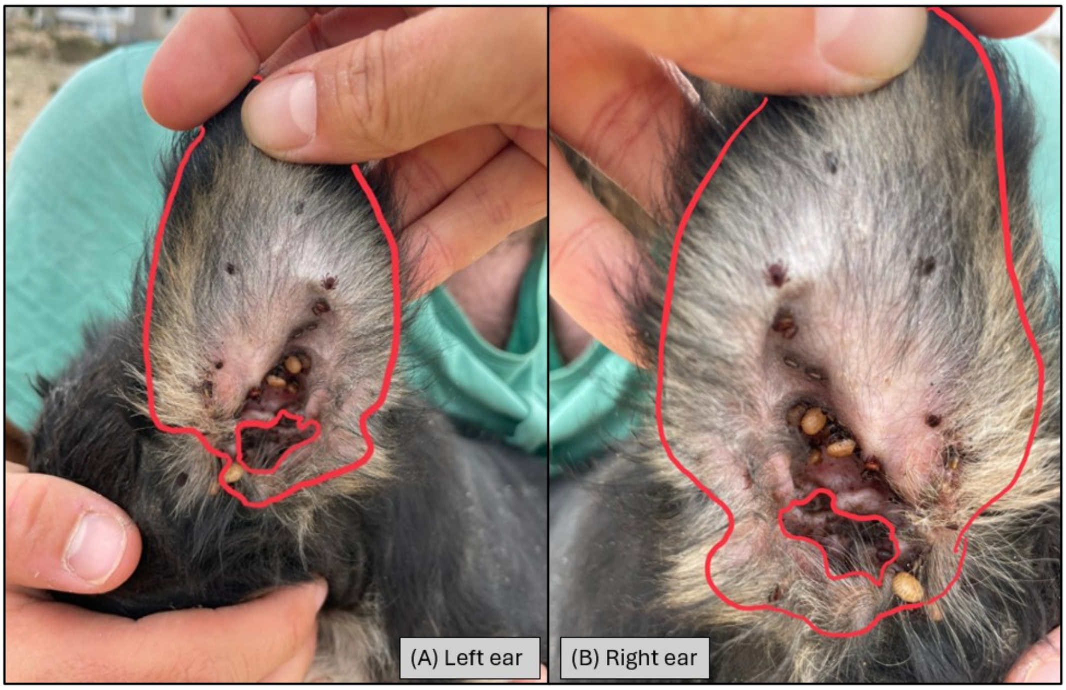

Figure 7. Counting ticks on the puppies' ears. Pictures from the field show examples of left (A) and right (B) ears.Counted was between the two red lines.

For both assessments, two people always counted the parasites, first independently and then together, to minimize human error.

8.2.4 Survival and Health Monitoring

Puppies were monitored for survival through regular visits during the daily scans and community reports. During measurements at the age of 3-, 5-, 8-, and 12-weeks data on body weight and body condition score (BCS) was recorded and taken as indicators for the overall health of the dog. For the assessment of the BCS, a 1-5 scale was used, with 1 indicating "very thin/starving" and 5 indicating "obese/fat" (Figure 8). BCS was determined through simple visual and haptic inspection, focusing on waist shape and, in particular, fat coverage over the ribs and pelvis, as suggested by German (2006) and Santarossa et al. (2017).

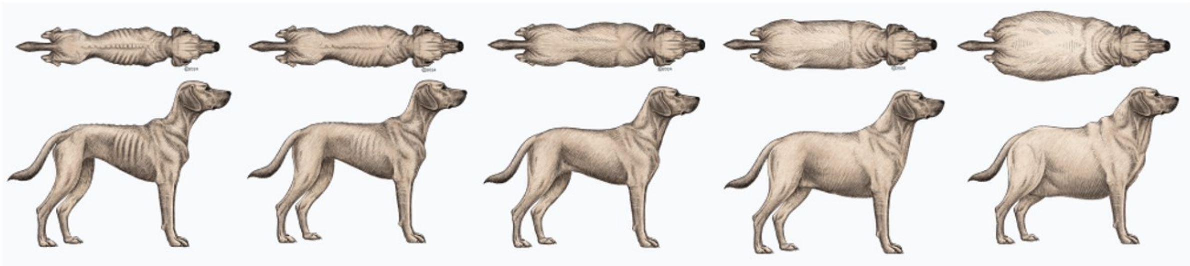

Figure 8. Five-point body condition score (BCS) system. Figure adapted from Association for Pet Obesity Prevention (2024), Body Condition Score for Dogs (BCS Chart) *(https://www.petobesityprevention.org/dogbcs) with permission, text descriptions also informed by Dorsten and Cooper (2004).*

8.3 Data Analysis

8.3.1 Software for Data Analysis

The recorded tests were video coded using the Behavioral Observation Research Interactive Software (BORIS) (Friard and Gamba, 2016). The software R version 4.4.1 (R Core Team, 2024) was used for statistical analysis.

8.3.2 Behavioral Analysis

To transfer the observed behaviors into personality traits, a behavioral scoring table was developed (Table A1 in the Appendix) that allowed us to weigh each behavior according to the personality trait. The interpretation of each behavior was based on a review of relevant literature (Table A1), as well as on the interpretation derived from the ethogram (e.g., biting, defined as “the pup *aggressively* bites …”) (Table A2 in the Appendix). Each behavior was assigned directional weights (positive, negative, neutral, or excluded) for sociability towards humans, sociability towards conspecifics, and boldness. Behaviors were z-scored (standardized) prior to applying trait weights to account for differences in scale and distribution. Human directed sociability scores were derived from Human Approach tests, conspecific directed sociability scores were derived from Fake Dog tests, and boldness scores were derived from Novel Object tests. For each trait, a weighted sum of the relevant z-scored behaviors was calculated, yielding a continuous trait index per puppy per test and age.

The ordinal values of activity level and first reaction were not captured through behavior frequency or duration and were integrated by applying a weighted system as well. Latency to approach (i.e. the time the puppy took to approach the stimulus in each test) was z-scored and while a longer latency reduced sociability and boldness indices, an additional penalty for puppies that never approached was also added.

8.3.3 Statistical Analysis

All analyses were performed in R version 4.4.1 (R Core Team, 2024). Core packages included *lme4* (Bates et al., 2015) for linear mixed models (LMM) and mixed-effects logistic regression; *ordinal* (Christensen, 2019) for cumulative-link mixed models (CLMM); *glmmTMB* (Brooks et al., 2017) for negative-binomial generalized linear mixed models (NB-GLMM) of flea and tick counts; *survival* (Therneau, 2015) for interval-censored, late-entry parametric survival models; and *ggplot2* (Wickham and Sievert, 2009) for visualization (boxplots, trait trends, survival curves, residual diagnostics).

8.3.3.1 Data preparation and response coding

Survival was analyzed both as a binary outcome and as time-to-event. For the binary outcome, mixed-effects logistic regression models were fit, with survival at 8 and 12 weeks coded as 1 (alive) or 0 (dead), with a random intercept for mother. For time-to-event analyses, survival was modeled as interval-censored, accounting for the uncertainty between checkups.

Continuous predictors were centered and scaled within age when used as z-scores. Categorical predictors (e.g., BCS) were treated as factors/ordinal as appropriate. For each model, rows with missing values in the variables required for that model were dropped.

8.3.3.2 Exploratory correlations Exploring correlations between personality traits, parasite counts, and body condition variables

As an overview, we screened pairwise associations among personality traits, parasite counts, and body condition variables at 5, 8, and 12 weeks. For each pair of variables at 5, 8, and 12 weeks we dropped rows with missing values, ran Shapiro-Wilk tests on each variable, and chose Pearson's r if both variables were approximately normal ($p > 0.05$) or Spearman's ρ otherwise. We considered correlations with $|\rho| > 0.35$ as moderate and $|\rho| > 0.5$ as strong. These screenings informed, but did not determine, subsequent mixed-model specifications.

8.3.3.3 Model classes and rationale

We used four complementary modeling frameworks, all with a random intercept for mother to account for litter effects:

1. **Linear mixed models (LMM) and cumulative-link mixed models (CLMM)**
   To test whether parasite burden influences later body condition, we used parasite counts from the preceding age as predictors and body condition variables as outcomes. For weight (continuous) as outcome we used LMM. Flea and tick counts were log-transformed and z-scored within age and then entered as predictors. We fit both "lag" models (e.g., 5-weeks parasites → 8-week weight) and baseline-adjusted models that

additionally included prior weight (e.g., weight at 5 weeks when modeling weight at 8 weeks) to quantify relative change in weight.

For Body Condition Score (BCS, ordinal 1-5) as outcome we used CLMM with proportional-odds link, using the same parasite predictors (log-transformed, z-scored within age).

2. **Negative-binomial generalized mixed models (NB-GLMM)**

   To test whether personality traits predict parasite burden, we modeled flea and tick counts (by age and parasite) using NB-GLMM with a random intercept for mother. Personality indices were z-scored within age and included as predictors.

3. **Mixed-effects logistic regression (alive vs. dead)**

   To test whether personality traits or parasite burden predicted survival to 8 or 12 weeks, we fit mixed-effects logistic regression models with a random intercept for mother.

4. **Interval-censored parametric survival models (late entry)**

   To investigate timing of death, we fit parametric models (Weibull and log-logistic accelerated failure time (AFT) forms) with interval censoring. These models estimate a continuous hazard function, accommodating cases where the exact time of death is unknown but only known to occur between two checkups. For all predictors (personality traits and parasite burden), we applied a late-entry design: only puppies alive at the predictor measurement age (35 days for 5-week predictors, 56 days for 8-week predictors) were included, and their risk time was reset to zero at that age. Thus, survival was modeled over the following observation windows: 0-21 days corresponding to ages 5-8 weeks, and 0-28 days corresponding to ages 8-12 weeks.

8.3.3.4 Model diagnostics and selection

All models were checked for convergence. In survival models, model fit was evaluated using Turnbull plots compared to fitted curves to model predictors (Figure A1 and A2 in the Appendix). Deviance residuals were inspected to check for model misfit (Figure A3 and A4 in the Appendix). No major violations were detected.

To avoid overfitting with limited n, we did not include interaction terms. Combined models that included both trait and parasite predictors were attempted but failed to converge due to small intersection of complete cases (n = 9) and were excluded.

For survival analyses, both Weibull and log-logistic AFT models were fit. Model comparisons were based on Akaike's Information Criterion (AIC) and Akaike weights (Table A2 in the Appendix). The log-logistic distribution allows for a non-monotonic hazard function, which may be biologically plausible in free-ranging dog puppies whose mortality risk might peak during weaning or early exploration before stabilizing. However, for consistency and interpretability, we report Weibull estimates in the main text unless otherwise justified.

We report effect sizes with 95% CI and $\alpha = 0.05$: regression coefficients for LMM (kg), odds ratios (OR) for CLMM/logistic models, incidence-rate ratios (IRR) for NB-GLMM, and time ratios (TR) for AFT survival models (TR > 1 indicates longer expected survival; TR < 1 shorter survival).

9 Results

9.1 Sex, Survival, and Sample Size

The 14 included litters consisted of 107 puppies of which 48 puppies (44.9%) were female, 55 puppies (51.4%) were male (Figure 9). The sex of 4 puppies (3.7%) was unknown because they died and disappeared before the age of 3 weeks, when we took them out of the den to determine the sex.

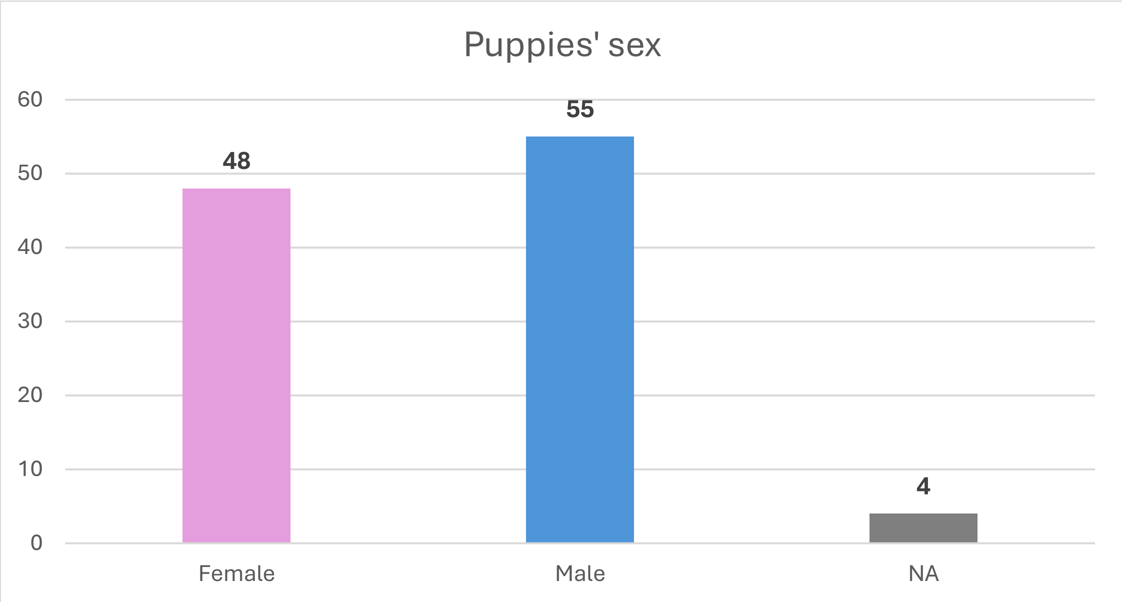

Figure 9. Distribution of the puppies' sex. Unknown sex in 4 cases because the puppies died and disappeared before the sex was identified.

103 puppies (96.3%) reached the age of 3 weeks, while 45 puppies (42.1%) were still alive at the age of 12 weeks, 52 puppies (48.6%) were dead, and 10 puppies (9.3%) got adopted until then (Figure 10).

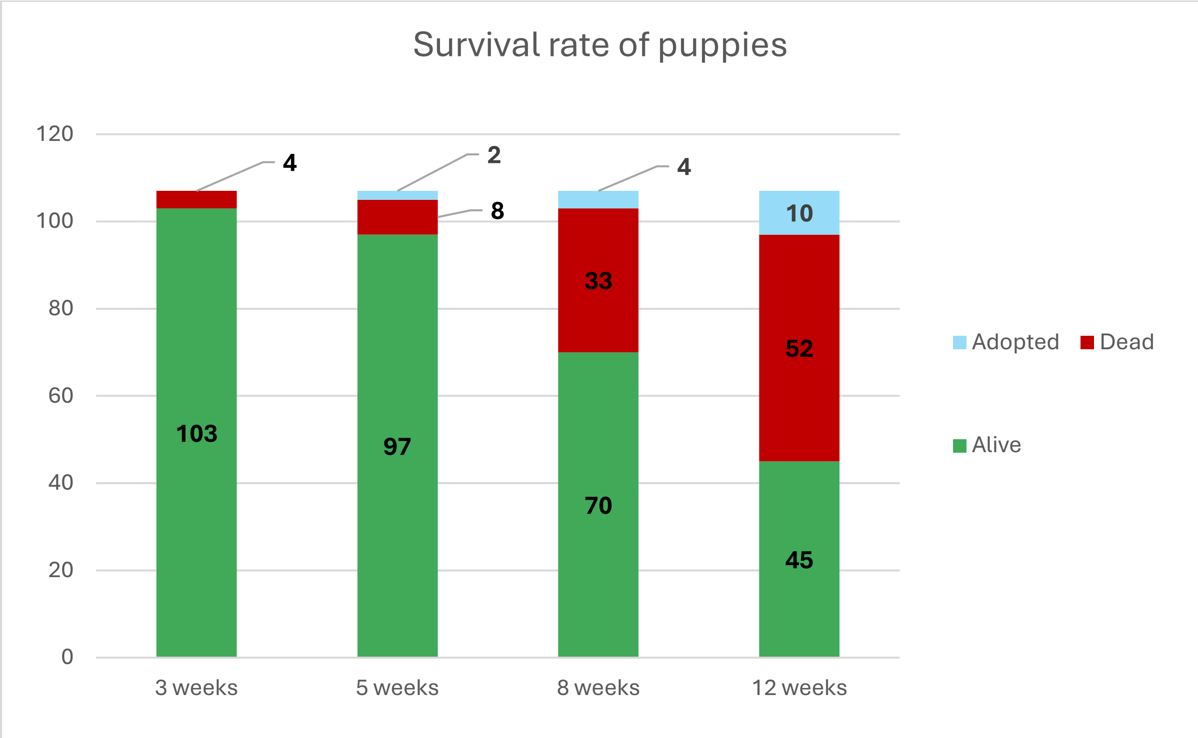

Figure 10. Survival rate of the puppies with adopted puppies included.

9.2 Descriptive Statistics

9.2.1 Comparison

No significant differences were found between ages in sociability towards humans (p = 0.089) or sociability towards conspecifics (p = 0.423) (Figure 11, Table 2). In contrast, boldness (as measured in the Novel Object test) showed a statistically significant decrease from 5 to 8 weeks (p = 0.038) (Figure 11, Table 2).

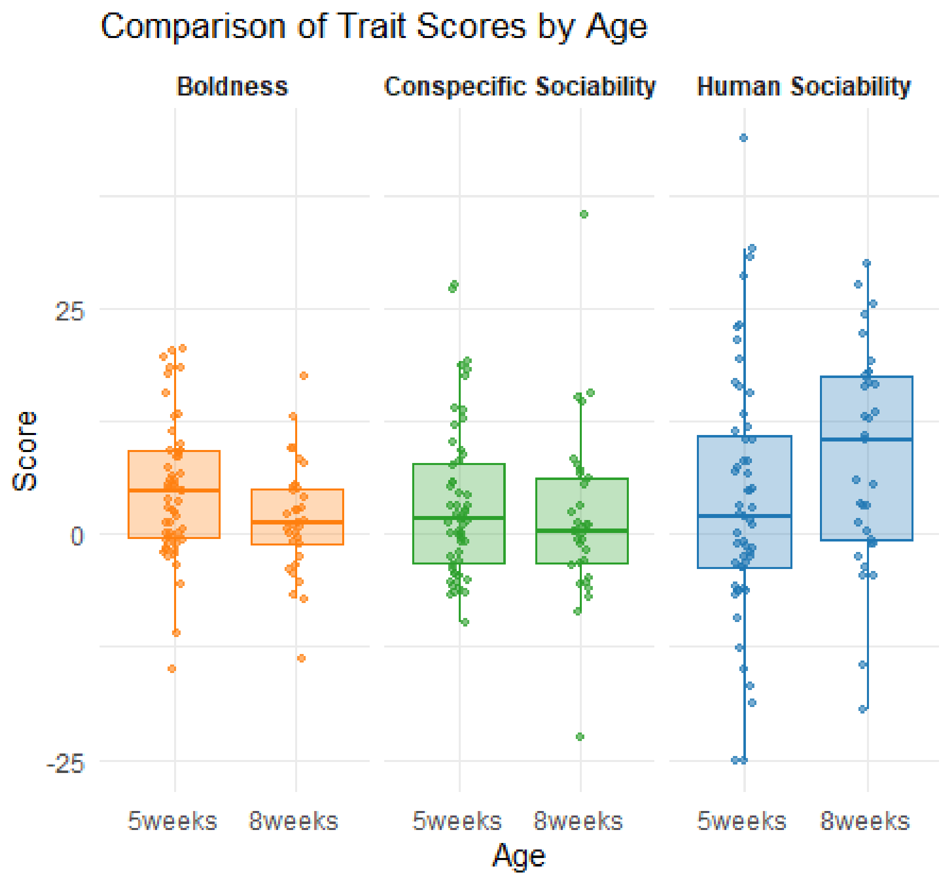

Figure 11. Distribution of personality trait scores by age.

Table 2. Distribution of personality trait scores across ages.

Trait	Normality	Test used	Mean (5w)	Mean (8w)	Test statistic	p-value
Soc_Hum	Normal ($p > 0.05$)	Welch's t-test	3.71	8.52	$t = -1.72$ df = 74.98	0.089
Soc_Con	Non-normal ($p < 0.02$)	Wilcoxon rank-sum	-	-	W = 1001	0.423
Boldness	**Normal ($p > 0.05$)**	**Welch's t-test**	**4.79**	**1.66**	**$t = 2.12$ df = 78.21**	**0.038**

No significant differences in flea counts across ages ($p = 0.411$), emerged (Figure 12, Table 3). For ticks, a weak trend was observed ($p = 0.082$), but this did not reach statistical significance (Figure 12, Table 3).

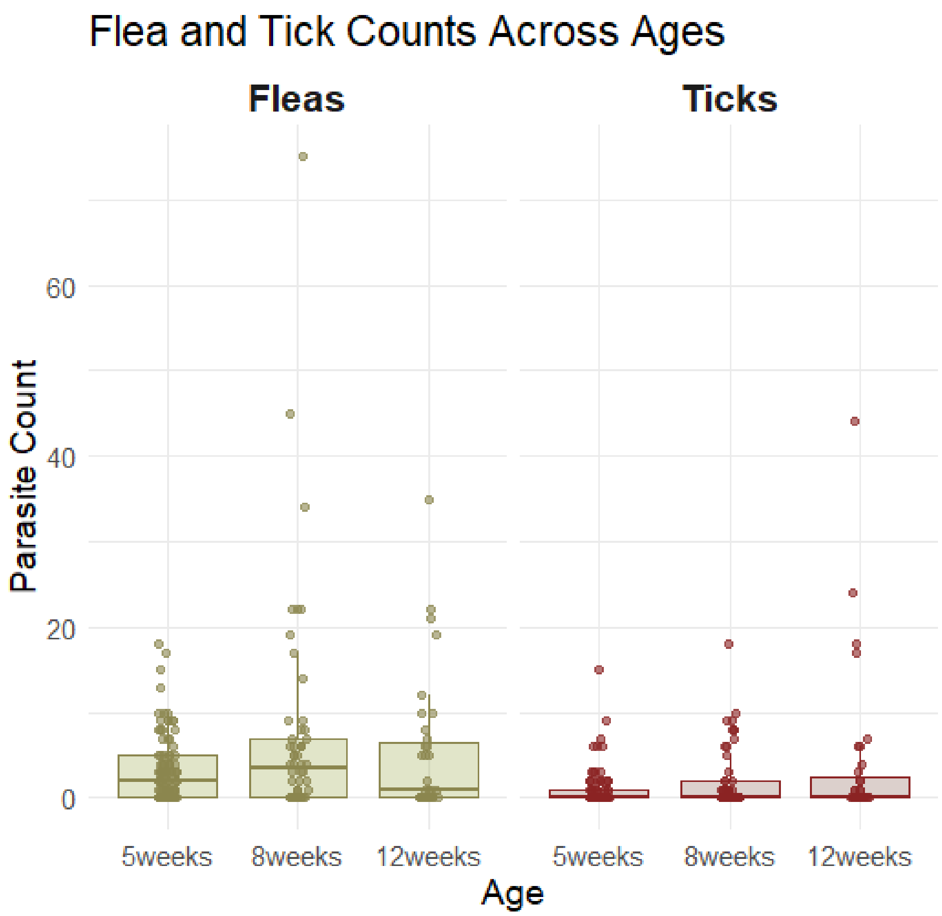

Figure 12. Distribution of flea and tick counts by age.

Table 3. Kruskal-Wallis tests comparing flea and tick counts across ages(5, 8, and 12 weeks).

Parasite	Test statistic (X^2)	df	p-value
Fleas	1.78	2	0.411
Ticks	4.99	2	0.082

9.2.2 Correlations between Personality Traits, Parasite Counts, and Body Condition Variables

No pair of personality traits and parasite counts at 5 weeks or 8 weeks showed a significant correlation (Table 4). At 12 weeks, however, a Spearman correlation between sociability towards conspecifics and tick burden was significant ($p = 0.050$) with a correlation coefficient of $\rho = 0.46$, indicating a moderately strong positive association ($|\rho| > 0.35$).

Table 4. Correlations between personality traits and parasite counts with correlation coefficients.

5 weeks Traits vs Parasites						
Variable 1	**Variable 2**	**Method**	**n**	**Correlation**	**p-value**	**Note**
Soc_Hum_5weeks	N_fleas_5weeks	spearman	55	-0.00	0.979	Non-normal data
Soc_Hum_5weeks	N_ticks_5weeks	spearman	55	-0.15	0.262	Non-normal data
Soc_Con_5weeks	N_fleas_5weeks	spearman	55	-0.15	0.274	Non-normal data
Soc_Con_5weeks	N_ticks_5weeks	spearman	55	-0.10	0.466	Non-normal data
Boldness_5weeks	N_fleas_5weeks	spearman	55	-0.13	0.364	Non-normal data
Boldness_5weeks	N_ticks_5weeks	spearman	55	-0.01	0.922	Non-normal data
8 weeks Traits vs Parasites						
Variable 1	**Variable 2**	**Method**	**n**	**Correlation**	**p-value**	**Note**
Soc_Hum_8weeks	N_fleas_8weeks	spearman	27	-0.08	0.681	Non-normal data
Soc_Hum_8weeks	N_ticks_8weeks	spearman	27	0.08	0.680	Non-normal data
Soc_Con_8weeks	N_fleas_8weeks	spearman	27	0.02	0.940	Non-normal data
Soc_Con_8weeks	N_ticks_8weeks	spearman	27	0.24	0.227	Non-normal data
Boldness_8weeks	N_fleas_8weeks	spearman	27	0.04	0.842	Non-normal data
Boldness_8weeks	N_ticks_8weeks	spearman	27	0.15	0.461	Non-normal data
12 weeks Traits vs Parasites						
Variable 1	**Variable 2**	**Method**	**n**	**Correlation**	**p-value**	**Note**
Soc_Hum_12weeks	N_fleas_12weeks	spearman	19	0.05	0.843	Non-normal data
Soc_Hum_12weeks	N_ticks_12weeks	spearman	19	-0.04	0.874	Non-normal data
Soc_Con_12weeks	N_fleas_12weeks	spearman	19	0.36	0.131	Non-normal data
Soc_Con_12weeks	**N_ticks_12weeks**	**spearman**	**19**	**0.46**	**0.050**	**Non-normal data**
Boldness_12weeks	N_fleas_12weeks	spearman	19	0.03	0.917	Non-normal data
Boldness_12weeks	N_ticks_12weeks	spearman	19	-0.02	0.928	Non-normal data

Several significant correlations were found between parasite counts and body condition variables (Table 5, 6, and 7). At 5 weeks (Table 5), the number of fleas showed significant ($p < 0.001$) and moderately strong positive associations with both the BCS ($\rho = 0.38$) and the weight of the puppy ($\rho = 0.40$). A further significant correlation ($p = 0.002$) was observed between the number of fleas and the mother's BCS, although this positive association was weaker ($\rho = 0.31$).

Table 5. Correlations between parasite counts and body condition variables at 5 weeks of age.

5 weeks Parasites vs Body Condition						
Variable 1	**Variable 2**	**Method**	**n**	**Correlation**	**p-value**	**Note**
Puppy_BCS_5weeks	**N_fleas_5weeks**	**spearman**	**96**	**0.38**	**0.000**	**Non-normal data**
Puppy_BCS_5weeks	N_ticks_5weeks	spearman	96	0.08	0.470	Non-normal data
Weight_5weeks	**N_fleas_5weeks**	**spearman**	**96**	**0.40**	**0.000**	**Non-normal data**
Weight_5weeks	N_ticks_5weeks	spearman	96	-0.11	0.294	Non-normal data
Mother_BCS_5weeks	**N_fleas_5weeks**	**spearman**	**96**	**0.31**	**0.002**	**Non-normal data**
Mother_BCS_5weeks	N_ticks_5weeks	spearman	96	0.09	0.384	Non-normal data

At 8 weeks, several significant correlations ($p < 0.015$) were found (Table 6). The number of fleas correlated strongly and positively with puppy weight ($\rho = 0.58$, $p < 0.001$), while the number of ticks correlated strongly and negatively (ρ = -0.49, p < 0.001). Puppy BCS was moderately and positively associated with flea counts (ρ = 0.33, p = 0.015). In contrast, mother BCS showed a strong and negative correlation with flea counts (ρ = -0.51, p = 0.001) and a strong positive correlation with tick counts (ρ = 0.72, p < 0.001).

Table 6. Correlations between parasite counts and body condition variables at 8 weeks of age.

8 weeks Parasites vs Body Condition						
Variable 1	Variable 2	Method	n	Correlation	p-value	Note
Puppy_BCS_8weeks	**N_fleas_8weeks**	**spearman**	**52**	**0.33**	**0.015**	**Non-normal data**
Puppy_BCS_8weeks	N_ticks_8weeks	spearman	52	0.19	0.168	Non-normal data
Weight_8weeks	**N_fleas_8weeks**	**spearman**	**52**	**0.58**	**0.000**	**Non-normal data**
Weight_8weeks	**N_ticks_8weeks**	**spearman**	**52**	**-0.49**	**0.000**	**Non-normal data**
Mother_BCS_8weeks	**N_fleas_8weeks**	**spearman**	**42**	**-0.51**	**0.001**	**Non-normal data**
Mother_BCS_8weeks	**N_ticks_8weeks**	**spearman**	**42**	**0.72**	**0.000**	**Non-normal data**

At 12 weeks, the moderate positive correlation between puppy BCS and flea counts observed at 8 weeks was even stronger (ρ = 0.55, p = 0.001) (Table 7). The positive correlation between mother BCS and tick counts also remained significant at 12 weeks, though weaker than at 8 weeks (ρ = 0.39, p = 0.041).

Table 7. Correlations between parasite counts and body condition variables at 12 weeks of age.

12 weeks Parasites vs Body Condition						
Variable 1	Variable 2	Method	n	Correlation	p-value	Note
Puppy_BCS_12weeks	**N_fleas_12weeks**	**spearman**	**35**	**0.55**	**0.001**	**Non-normal data**
Puppy_BCS_12weeks	N_ticks_12weeks	spearman	35	0.31	0.073	Non-normal data
Weight_12weeks	N_fleas_12weeks	spearman	20	0.19	0.436	Non-normal data
Weight_12weeks	N_ticks_12weeks	spearman	20	-0.09	0.698	Non-normal data
Mother_BCS_12weeks	N_fleas_12weeks	spearman	28	0.27	0.167	Non-normal data
Mother_BCS_12weeks	**N_ticks_12weeks**	**spearman**	**28**	**0.39**	**0.041**	**Non-normal data**

9.2.3 Linear, Cumulative-Link, and Negative-Binomial Generalized Mixed Models

9.2.3.1 Linear mixed models and cumulative-link mixed models (parasites → body condition)

After accounting for litter effects (random intercept mother), there is no robust evidence that higher flea or tick burden at 5 weeks or 8 weeks predicts lower subsequent body weight (Table 8). In the baseline-adjust models, prior weight shows the positive association with later weight.

Table 8. Linear mixed models of later weight on earlier parasite burden. Baseline-adjusted rows include baseline weight. Coefficients are kg differences in later weight per 1-SD increase in log parasite count (log counts z-scored within age). Random intercept for mother. Abbreviations: z_logFleas5w = z-scored log(flea count) at 5 weeks; z_logTicks5w = z-scored log(tick count) at 5 weeks; analogous notation for 8 weeks.

Outcome	Model	Predictor	Estimate (95% CI)	p-value	n	AIC
8w weight	lag	z_logFleas5w	0.26 (-0.04 - 0.56)	0.086	57	152.36
8w weight	lag	z_logTicks5w	-0.03 (-0.28 - 0.22)	0.792	57	152.36
8w weight	**baseline-adj**	**Weight_5w**	**1.55 (1.27 - 1.82)**	**< 0.001**	**57**	**89.64**
8w weight	baseline-adj	z_logFleas5w	0.02 (-0.15 - 0.20)	0.789	57	89.64
8w weight	baseline-adj	z_logTicks5w	0.04 (-0.10 - 0.17)	0.541	57	89.64
12w weight	lag	z_logFleas8w	-1.62 (-5.74 - 2.50)	0.441	16	113.34
12w weight	lag	z_logTicks8w	0.23 (-2.46 - 2.92)	0.867	16	113.34
12w weight	baseline-adj	Weight_8w	2.46 (-0.77 - 5.69)	0.135	16	113.25
12w weight	baseline-adj	z_logFleas8w	-2.64 (-6.73 - 1.44)	0.205	16	113.25
12w weight	baseline-adj	z_logTicks8w	1.23 (-1.61 - 4.07)	0.397	16	113.25

Ordinal BCS models (CLMM) show no clear association between earlier parasite burden and later BCS (Table 9). The 12-week models were unstable due to small n.

Table 9. Cumulative-link mixed models of later BCS on earlier parasite burden. Estimates shown as odds ratios (OR) per 1-SD increase in log parasite count (log counts z-scored within age). Random intercept for mother. NA = non-convergence/unstable SE. Abbreviations: z_logFleas5w = z-scored log(flea count) at 5 weeks; z_logTicks5w = z-scored log(tick count) at 5 weeks; analogous notation for 8 weeks.

Outcome	Model	Predictor	OR (95% CI)	p-value	n	AIC
bcs8_lag	lag	z_logFleas5	2.11 (0.36 - 12.57)	0.411	57	65.285
bcs8_lag	lag	z_logTicks5	1.49 (0.34 - 6.56)	0.595	57	65.285
bcs12_lag	lag	z_logFleas8	NA	NA	21	22.533
bcs12_lag	lag	z_logTicks8	NA	NA	21	22.533

9.2.3.2 Negative-binomial generalized mixed models (personality traits → parasites)

Trait models suggest a behavioral exposure signal at 8 weeks. Pups with higher conspecific sociability had higher flea and tick counts, while human sociability and boldness were not clearly related (Table 10). All models include a random intercept for mother. Trait indices were z-scored within age.

Table 10. Negative-binomial generalized mixed models of parasite counts on personality traits, by age and parasite. Effects shown as incidence rate ratios (IRR) per 1-SD increase in trait score (traits z-scored within age). Random intercept for mother.

Outcome	Age	Predictor	IRR (95% CI)	p-value	n	AIC
Fleas	5w	zSoc_Hum	1.14 (0.87 - 1.49)	0.350	55	288.17
Fleas	5w	zSoc_Con	0.89 (0.71 - 1-11)	0.299	55	288.17
Fleas	5w	zBold	0.91 (0.71 - 1.18)	0.480	55	288.17
Ticks	5w	zSoc_Hum	1.34 (0.75 - 2.41)	0.320	55	154.48
Ticks	5w	zSoc_Con	0.67 (0.36 - 1.25)	0.210	55	154.48
Ticks	5w	zBold	0.94 (0.57 - 1.55)	0.814	55	154.48
Fleas	8w	zSoc_Hum	0.82 (0.53 - 1.28)	0.388	27	134.21
Fleas	**8w**	**zSoc_Con**	**1.40 (1.03 - 1.89)**	**0.031**	**27**	**134.21**
Fleas	8w	zBold	0.84 (0.59 - 1.19)	0.323	27	134.21
Ticks	8w	zSoc_Hum	0.70 (0.46 - 1.07)	0.097	27	103.91
Ticks	**8w**	**zSoc_Con**	**1.49 (1.20 - 1.85)**	**0.000**	**27**	**103.91**
Ticks	8w	zBold	0.92 (0.65 - 1.29)	0.613	27	103.91
Fleas	12w	zSoc_Hum	1.30 (0.78 - 2.17)	0.310	19	111.92
Fleas	12w	zSoc_Con	0.81 (0.50 - 1.32)	0.393	19	111.92
Fleas	12w	zBold	1.28 (0.79 - 2.07)	0.318	19	111.92
Ticks	12w	zSoc_Hum	0.67 (0.29 - 1.56)	0.349	19	108.75
Ticks	12w	zSoc_Con	1.86 (0.80 - 4.32)	0.152	19	108.75
Ticks	12w	zBold	0.55 (0.27 - 1.14)	0.110	19	108.75

9.2.4 Effects of Personality Traits on Survival (Mixed-Effects Logistic Regression)

We found no evidence that boldness or sociability traits significantly influenced puppy survival in any of the models tested, as the visualizations already indicated (Figure 13 and Figure 14).

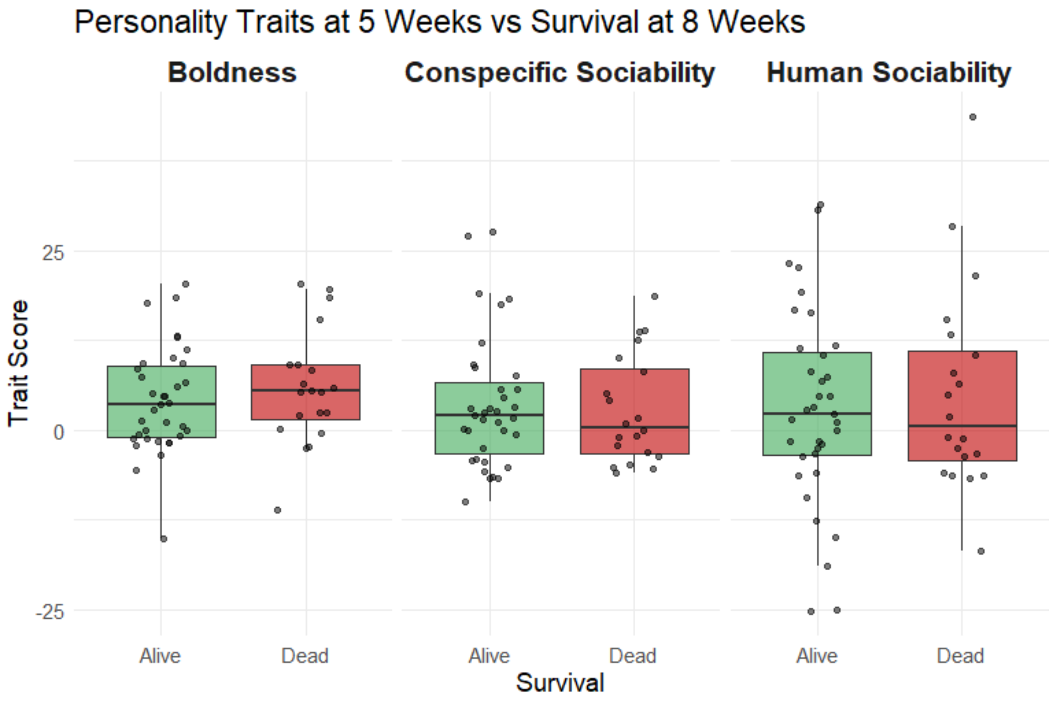

Figure 13. Distribution of personality trait scores at 5 weeks of age by survival at 8 weeks.

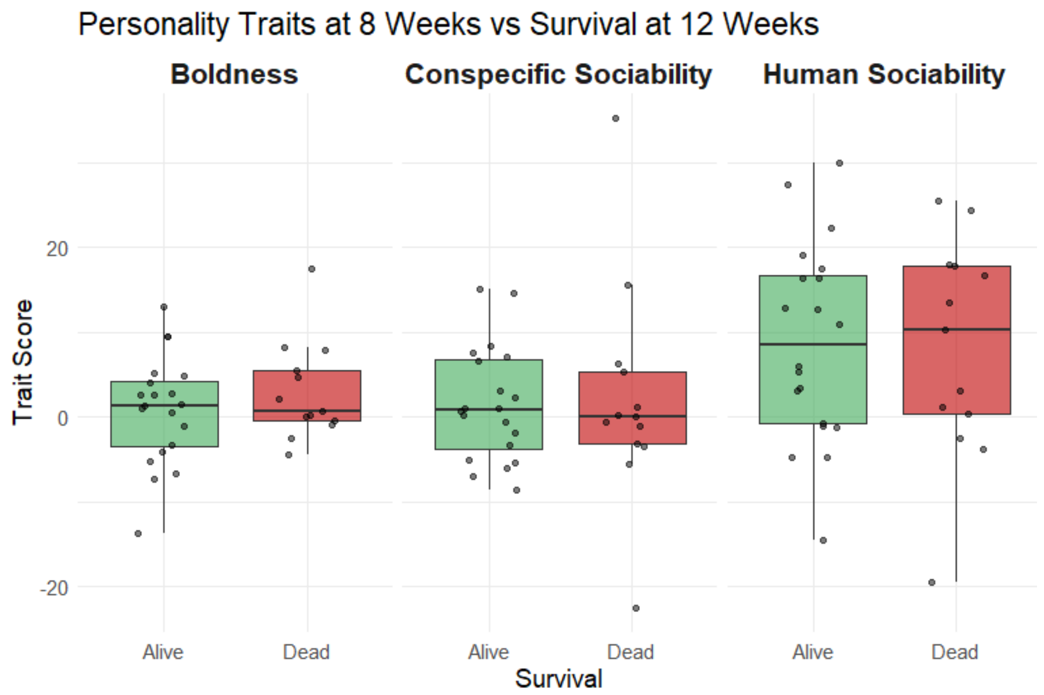

Figure 14. Distribution of personality trait scores at 8 weeks of age by survival at 12 weeks.

In the mixed-effects logistic regression models (accounting for mother as a random effect), odds ratios (OR) for all trait predictors were close to 1, and 95% confidence intervals consistently included 1, indicating null effects (Table 11). This held across models predicting survival at both 8 and 12 weeks from traits measured at 5 and 8 weeks.

Table 11. Mixed-effects logistic regression results for trait predictors. Odds ratios (OR), 95% confidence intervals, and p-values are shown for models linking personality traits to binary survival outcomes. All models include a random intercept for mother.

Model	Predictors	Response	OR (95% CI)	p-value	n
Traits 5w → 8w	Boldness_5weeks, Soc_Hum_5weeks, Soc_Con_5weeks	Survive 8w	0.94 (0.85 -1.04); 0.95 (0.89 -1.01); 1.02 (0.94 -1.11)	0.248; 0.124; 0.631	55
Traits 5w → 12w	Boldness_5weeks, Soc_Hum_5weeks, Soc_Con_5weeks	Survive 12w	1.03 (0.94 -1.13); 0.98 (0.93 -1.04); 0.97 (0.90 -1.05)	0.472; 0.510; 0.482	55
Traits 8w → 12w	Boldness_8weeks, Soc_Hum_8weeks, Soc_Con_8weeks	Survive 12w	0.82 (0.60 -1.12); 1.10 (0.90 -1.33); 0.99 (0.88 -1.11)	0.211; 0.350; 0.851	33

9.2.5 Effects of Parasite Burden on Survival (Mixed-Effects Logistic Regression)

As the visualization of parasite burden and survival already suggests (Figure 15 and 16), there were no clear associations found.

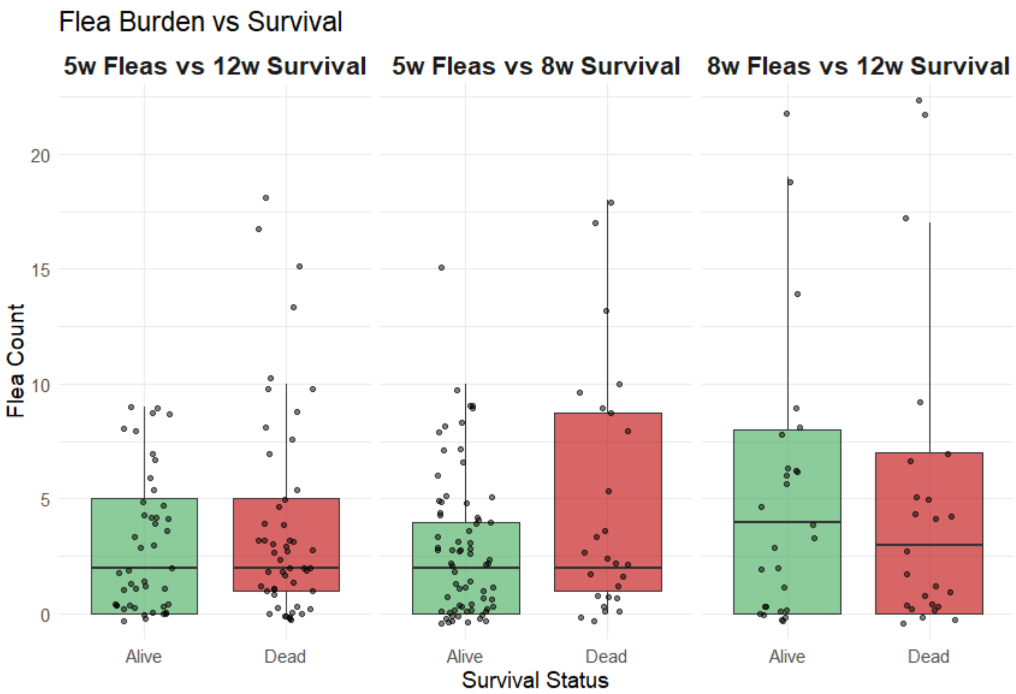

Figure 15. Distribution of flea counts at 5 or 8 weeks of age by survival status at subsequent ages (8 or 12 weeks). Flea counts were only available from living puppies at the time of assessment; thus, earlier flea burdens were compared with later survival outcomes. Extreme outliers hidden.

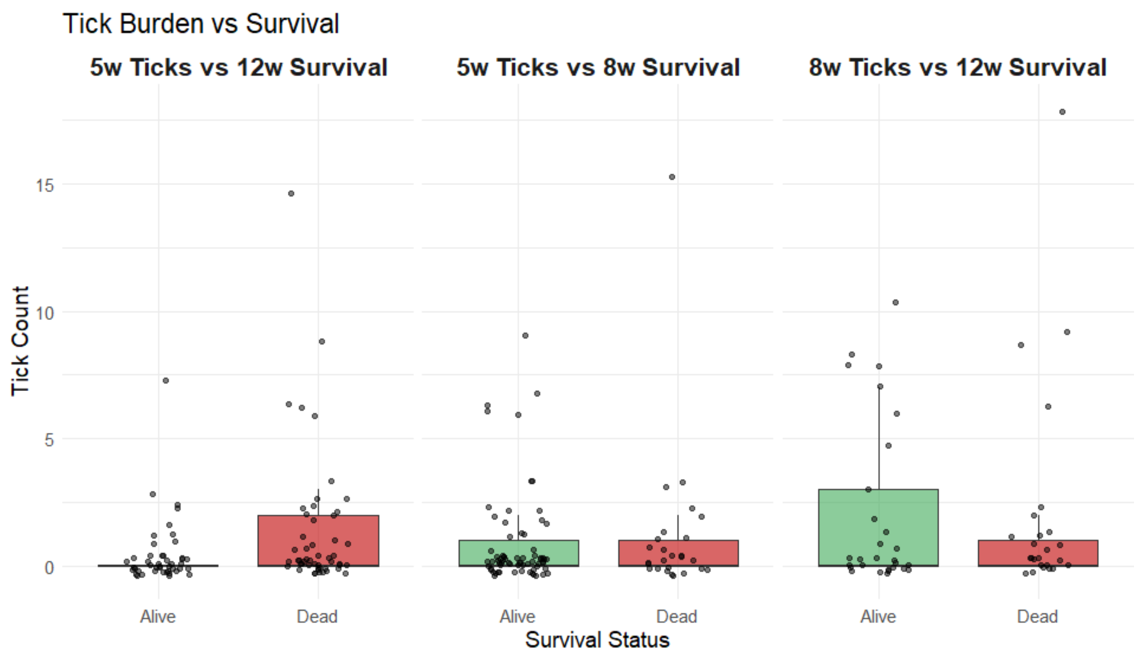

Figure 16. Distribution of tick counts at 5 or 8 weeks of age by survival status at subsequent ages (8 or 12 weeks). Tick counts were only available from living puppies at the time of assessment; thus, earlier tick burdens were compared with later survival outcomes.

In the mixed-effects logistic regression models (accounting for mother as a random effect), none of the parasite predictors (tick or flea counts at 5 or 8 weeks) were significantly associated with survival to 8 or 12 weeks (all $p > 0.1$). Odds ratios were again close to 1, and all 95% confidence intervals included 1 (Table 12).

Table 12. Mixed-effects logistic regression results for parasite burden predictors. Odd ratios (OR), 95% confidence intervals, and p-values are shown for models linking parasite burden to binary survival outcomes. All models include a random intercept for mother.

Model	Predictors	Response	OR (95 % CI)	p-value	n
Paras. 5w → 8w	N_fleas_5weeks, N_ticks_5weeks	Survive 8w	0.95 (0.80 -1.13); 1.05 (0.78 -1.43)	0.566; 0.738	96
Paras. 5w → 12w	N_fleas_5weeks, N_ticks_5weeks	Survive 12w	0.92 (0.78 -1.09); 0.74 (0.51 -1.07)	0.359; 0.106	96
Paras. 8w → 12w	N_fleas_8weeks, N_ticks_8weeks	Survive 12w	1.02 (0.97 -1.07); 1.00 (0.86 -1.16)	0.455; 0.999	54

9.3 Personality Traits, Parasite Burden and Survival (Interval-Censored AFT)

9.3.1 Survival Models in General

All survival models were estimated in a late-entry accelerated-failure-time (AFT) framework: Only puppies alive at the age when predictors were measured were included (35 days for

5-week predictors, 56 days for 8-week predictors). Full model selection details are in the Appendix in Table A3 and model coefficients are reported in Table A4.

9.3.2 5-Week Predictors (Survival 35-56 Days)

The Weibull model was strongly preferred for personality traits measured at 5 weeks (AIC = 428.8; weight = 0.92), outperforming the log-logistic alternative (ΔAIC = 4.8). None of the personality traits predicted survival during this interval (all $p > 0.19$). Parasite-only models at 5 weeks were not supported (ΔAIC ≥ 226; all $p > 0.11$).

9.3.3 8-Week Predictors (Survival 56-84 Days)

For personality traits measured at 8 weeks, model fit was nearly identical between Weibull and log-logistic distribution (AIC = 130.3 vs 130.3; ΔAIC = 0.02; weights = 0.50 vs 0.50). As in the earlier window, no personality trait significantly predicted survival (all $p > 0.37$). Parasite-only models for 8-week predictors were also unsupported (ΔAIC > 128) and yielded no significant effects (all $p > 0.5$).

Nevertheless, a slightly slower decrease in survival probability can be observed in puppies with low boldness scores (Figure 17 A). For sociability towards humans, there is almost no visible difference between the survival curves of puppies with high and low scores (Figure 17 C). In contrast, puppies with high conspecific sociability scores show a slightly slower decline in survival probability compared to those with low scores (Figure 17 E).

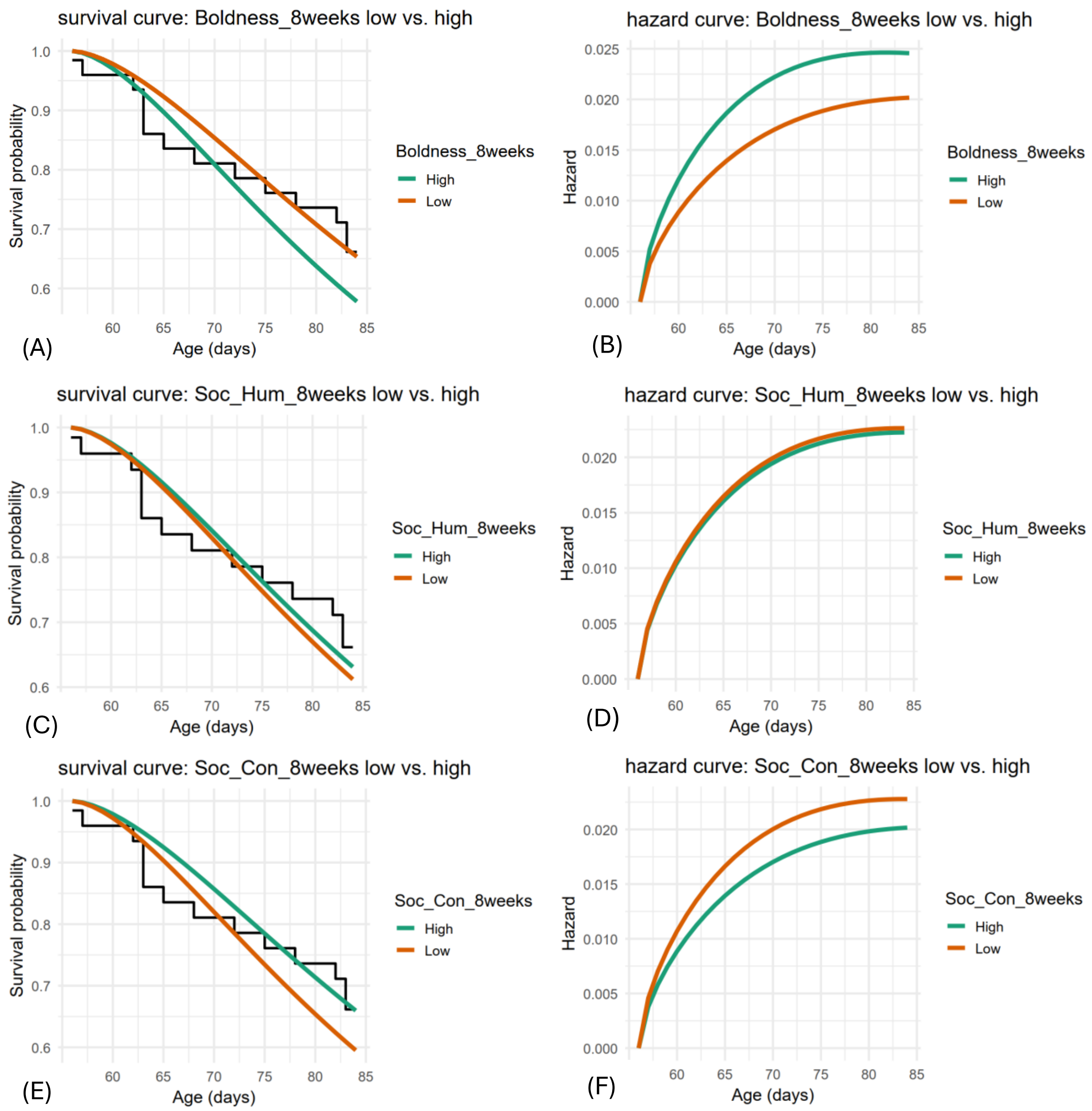

Figure 17. Survival curves for the different personality traits (boldness A, sociability towards humans C, sociability towards conspecifics E) and hazard curves for the different personality traits (boldness B, sociability towards humans D, sociability towards conspecifics F) at the age of 8 weeks with high (= 75th percentile) and low (= 25th percentile) scores.

A similar pattern is evident in the hazard curves: puppies with high scores in boldness or conspecific sociability exhibit a faster increase in hazard over time (Figure 17 B and F), whereas sociability towards humans appears to have little influence on the risk of dying (Figure 17 D).

10 Discussion

10.1 General

This study investigated whether personality traits in free-ranging dog puppies predict ectoparasite burden or survival during the first 12 weeks of life. Additionally, we examined whether earlier parasite burden forecasts later body condition. Survival models using personality traits should be interpreted with caution, as these traits are not yet fixed in early development and show only short-term stability that increases with age (Barnard et al., 2016; Fratkin et al., 2013; Riemer et al., 2014). Accordingly, traits measured at 5 weeks may still be in flux and thus less reliable for predicting later outcomes, whereas those assessed at 8 weeks are more likely to remain stable over the period up to 12 weeks of age (MacDonald, 1983). CIs were wide in several models, indicating imprecision compatible with small to moderate effects in either direction. Given the number of tests, we emphasize patterns replicated across ages or methods over single p-values.

10.2 Key Findings

Across analyses that accounted for non-independence within litters (random intercept for mother), three patterns emerged. First, ectoparasite loads were broadly stable across ages and did not robustly depress later weight or alter BCS in mixed models. Second, at 8 weeks, higher conspecific sociability was associated with higher flea and tick counts. Third, neither traits nor ectoparasite burden predicted survival to 8 or 12 weeks in mixed-effects logistic or accelerated failure time AFT survival analyses.

These results do not support the hypotheses that (1) more sociable and bold puppies would have lower ectoparasite burdens, or that (2) sociable traits towards both conspecifics and humans, as well as bold traits would be associated with higher survival rates within the 12-week observation period. Instead, the trait–parasite association that emerged was in the opposite direction at 8 weeks, with greater conspecific sociability being related to a higher parasite burden.

10.3 Parasite Burden

Do traits predict parasite burden? Partly – at 8 weeks only. Puppies with higher conspecific sociability carried more fleas and ticks, while boldness and human sociability showed no clear links. In negative-binomial models at 8 weeks, conspecific sociability predicted higher counts for fleas (IRR = 1.40; $p = 0.031$) and ticks (IRR = 1.49; $p < 0.001$). An IRR of 1.49 indicates approximately 49% higher expected tick counts per 1-SD increase in conspecific sociability at 8 weeks. An IRR of 1.40 indicates approximately 40% higher expected flea counts.

Descriptively, the 12-week Spearman correlation between conspecific sociability and ticks ($\rho = 0.46$; $p = 0.050$) is consistent with a moderately strong positive association.

Why might the 8-week signal appear? This point coincides with wider exploration and peer play, plausibly increasing contact-mediated exposure. Biologically, several mechanisms could underlie the 8-week sociability signal: closer contact rates among conspecifics, shared bedding, and social play can facilitate ectoparasite transfer. This aligns with studies showing that closer proximity to conspecifics and a greater diversity of contacts increase the risk of parasite infestation and infection (Presley, 2011; Richards, 2010; Wilson-Aggarwal et al., 2019). Grooming can also substantially reduce ectoparasites across species (Addison et al., 2019; Mooring et al., 1996). Maternal and allogrooming may therefore mitigate burdens, however, their frequency and efficacy were not quantified here. Given reports that dogs can be inefficient at removing ectoparasites (Abrantes, 1997), variation in social contact may outweigh grooming benefits in this age window. A focused investigation of grooming efficacy in dogs would be valuable for understanding grooming as social behavior and hygiene. Future studies should also consider the ecology of ectoparasites, which depends not only on host characteristics (e.g., sex, age, body weight), but also on season and the host's environment (Benedek et al., 2024; Krasnov et al., 2004; Obiegala et al., 2021).

Do earlier parasites forecast later condition? Not clearly in this cohort. LMM and CLMM indicated no robust prospective effects of flea or tick counts measured at 5 or 8 weeks on subsequent weight or BCS. In baseline-adjusted models, prior weight strongly predicted later weight, as expected for growth tracking, while parasite effects were small and imprecise. This implies that any cross-sectional links between condition and parasites did not translate into detectable short-term impacts on growth or BCS. These findings do not align with some prior work. For example, Mooring (2024) and Norval et al. (1988) described weight loss, impaired growth, and anorexia caused by infestations with ectoparasites like ticks. However, we must note that our focus for this study was on personality traits affecting ectoparasite burdens and survival. Therefore, our body-condition data were limited to body weight and a relatively coarse BCS scale (1-5) to track variables like growth and health. Future research interested in ectoparasite effects on body development should consider more variables like body dimensions (e.g., body length and body height) and a refined BCS scale (e.g., the 9-point scale proposed by Laflamme (1997)) to track growth. Future research could also consider assessing clinical parameters (e.g., anemia, heart rate, lethargy).

10.4 Survival

Do traits or ectoparasites predict short-term survival? No clear associations were detected. In mixed-effects logistic models, Ors for trait and parasite predictors were near 1 with 95% Cis spanning 1, and interval-censored AFT models likewise showed no significant effects at 5 to 8 weeks or 8 to 12 weeks. This may reflect the overriding influence of external factors, particularly human intervention, which was a major cause of puppy disappearance and mortality (e.g., culling, adoption, displacement), and biological stressors (e.g., endoparasites like *Echinococcus granulosus*, or infectious diseases such as parvovirus or rabies). In such contexts, intrinsic traits and ectoparasites may exert only marginal effects over the short observation window.

Our results do not provide evidence for the theory that immune function is linked to ectoparasite infestation (Benedek et al., 2024; Obiegala et al., 2021). If that linkage were strong and immediate in this population and timeframe, we would expect pups with heavier ectoparasite loads to show poorer body condition and lower survival. We did not detect such patterns. This leaves open the possibility that the link is distal, weaker, or masked by other factors (e.g., human interference, disease, maternal care).

The null survival results do not imply a lack of biological relevance. Limited statistical power, unmeasured covariates (e.g., pathogen load, maternal care), short-term observation, and complex trait-environment interactions may obscure modest effects that manifest only under long-term observation and specific challenges (e.g., drought, disease outbreaks), which exceeded the scope and feasibility of this study.

10.5 Limitations and Future Directions

Several limitations must be noted. First, behavioral tests were constrained by field logistics, leading to missing data, potential observer bias, and interruptions (e.g., weather, people, or other dogs). Second, the analysis was underpowered to detect small or interactive effects, particularly in survival models. Third, although the behavioral indices were carefully constructed and informed by literature, trait expression may still have been influenced by context (e.g., fatigue, ambient temperature). For instance, differentiating appeasement or submissive behavior from low sociability has been difficult, possibly leading to underestimation of sociability. These issues were also discussed by Pastore et al. (2011), who investigated behavioral stress-dependent parameters in agility dogs and noted that some of the displacement behavior they observed (e.g., yawning, lip licking) could equally have represented appeasement behavior. Bryce et al. (2024), who investigated the meaning of body shaking behavior in dogs, note that there is no “true dictionary of dog behaviors” and that basic behaviors have not been studied, which may lead to misinterpretation.

Future research could address the limitations by increasing sample size considerably, which would make a principal component analysis (PCA) possible and reduce the need for a potentially misinterpreted scoring of each single behavior. To yield a more holistic understanding of early-life survival drivers in free-ranging dogs, parameters such as the timing of individual weaning, cause of death, maternal behavior, or social network structure should be included.

Empirical investigation into puppy behavior could also contribute to a deeper understanding of single behaviors and help develop a refined ethogram. As highlighted by Bryce et al. (2024), scientific knowledge of dog behavior remains limited, especially for puppies, whose behavioral expressions differ from adults' (Abrantes, 1997).

11 Conclusion

Pups that were more sociable with conspecifics at 8 weeks tended to carry more ectoparasites, but we found no evidence that earlier parasite burden impaired short-term growth or BCS, nor that traits or parasites predicted survival within the first 12 weeks. These results point to behavioral exposure as a plausible driver of parasite load at a specific developmental stage, while suggesting that growth and survival in free-ranging puppies are likely dominated by broader environmental and anthropogenic factors.

The study contributes baseline evidence to animal personality research under field conditions. The findings suggest that personality traits, at least as measured under field conditions in early puppyhood, may not exert strong direct effects on short-term survival and show only limited, age-specific links to parasite burden. Instead, external environmental and human factors likely play dominant roles during this vulnerable period. Nonetheless, the age-specific association between conspecific sociability and ectoparasite burden points to complex interactions that merit further investigation.

Understanding how early behavioral traits interact with environmental risks is relevant for ecology and One Health. Future studies with larger cohorts, longer follow-ups, and integrative approaches (e.g., maternal care, environmental conditions, disease outbreaks, social network analysis) could yield deeper insights into how individual differences influence health outcomes across species and contexts.

Although the sample size was too small to draw definitive conclusions, it highlights both the feasibility and the scientific value of conducting personality assessments under field conditions in young free-ranging animals. This work serves as a stepping stone for future research into the ecological and behavioral foundations of early survival.

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Appendix

Table A1. Personality trait scoring table.

Behavior	Type	Modifier	Sociability	Boldness	Scoring Explanation	Literature
Activity level	Ordinal	1 - inactive	-1	-1	Disengaged; potential shutdown	See ethogram
Activity level	Ordinal	2 - weakly active	-1	-1	Low curiosity; stress or withdrawal	See ethogram
Activity level	Ordinal	3 - active	+1	+1	Engaged but balanced activity	See ethogram
Activity level	Ordinal	4 - very active	+1	+1	High energy; confident exploration	See ethogram
Activity level	Ordinal	5 - overactive	0	+1	Overactive; potentially impulsive or bold; less socially directed	See ethogram
Barking	Dur	E1/E2	-1	excluded	Offensive or defensive aggression	Bradshaw et al., 2016
Barking	Dur	E1/E2+toy	-1	excluded	Offensive or defensive aggression	Bradshaw et al., 2016
Barking	Dur	FD	-1	excluded	Offensive or defensive aggression	Bradshaw et al., 2016
Barking	Dur	NO	excluded	-1	Offensive or defensive aggression	Bradshaw et al., 2016
Barking	Dur	Toy	0	0	Not relevant for sociability or boldness scoring	-
Biting	Freq	E1/E2+toy	-1	excluded	Sign of fear and anxiety or aggression	Abrantes, 1997; Loftus et al., 2012
Body Shaking	Freq		-1	-1	Stress-release signal	Pastore et al., 2011
Body contact	Dur	E1/E2	+1	excluded	Affiliative closeness; social comfort; communication (e.g. musslze-nudge)	Abrantes, 1997
Body contact	Dur	E1/E2+toy	+1	excluded	Affiliative closeness; social comfort; communication (e.g. musslze-nudge)	Abrantes, 1997
Body contact	Dur	FD	+1	excluded	Affiliative closeness; social comfort; communication (e.g. musslze-nudge)	Abrantes, 1997
Body contact	Dur	NO	excluded	+1	Engagement or comfort with target	
Body contact	Dur	Toy	0	+1	Engagement or comfort with target	
Carrying toy	Dur		0	-1	Displacement activity	Abrantes, 1997
Climb on person	Dur		+1	excluded	Affiliative closeness; social comfort	Abrantes, 1997
Close proximity	Dur	Door	-1	-1	Directed towards exit (anxiety or fear)	Loftus et al., 2012
Close proximity	Dur	E1/E2	+1	excluded	Positive social engagement	Derived from body contact as it is a similar behavior
Close proximity	Dur	E1/E2+toy	+1	excluded	Positive social engagement	Derived from body contact as it is a similar behavior
Close proximity	Dur	Fake dog	+1	excluded	Positive social engagement	Derived from body contact as it is a similar behavior
Close proximity	Dur	Novel object	excluded	+1	Engagement or comfort with target	
Crouch	Dur		-1	-1	Fear/submissive posture	Bradshaw et al., 2016; Schenkel, 1947
First reaction HA/FD/NO	Category	AG = Approach Aggressive	-2	+1	Negative for sociability but positive for boldness as it is an approach, despite being conflict-driven	See ethogram
First reaction HA/FD/NO	Category	FE = Approach Fearful	-1	+1	Negative for sociability but positive for boldness (hesitant but still confronts the stimulus, indicative of boldness under stress)	See ethogram

First reaction HA/FD/NO	Category	FR = Approach Friendly	+2	+2	Very sociable and bold/confident sign	See ethogram
First reaction HA/FD/NO	Category	FRE = Freeze	-2	-2	Sign of fear and anxiety	Loftus et al., 2012
First reaction HA/FD/NO	Category	MA = Avoidance mild avoidance	-1	-1	Potential sign of fear and anxiety; not sociable or bold	Abrantes, 1997; Loftus et al., 2012
First reaction HA/FD/NO	Category	None	excluded	excluded		-
First reaction HA/FD/NO	Category	RI = Approach Rigid	-1	+1	Dominant or aggressive behavior; negative for sociability but positive for boldness as it is an approach	Abrantes, 1997
First reaction HA/FD/NO	Category	SA = Avoidance strong avoidance	-2	-2	Potential sign of fear and anxiety; not sociable or bold	Abrantes, 1997; Loftus et al., 2012
First reaction HA/FD/NO	Category	UN = Uncertain	excluded	excluded		-
Gazing	Dur	E1/E2	+1	excluded	Gaze aversion when anxious	Bradshaw et al., 2016; Pastore et al., 2011
Gazing	Dur	Helper	0	0	Not relevant for sociability or boldness scoring	-
Gazing	Dur	None	excluded	excluded		-
Genital sniffing	Freq		+1	excluded	Conspecific social interaction; greeting behavior	Abrantes, 1997; Schenkel, 1947
Growling	Freq	E1/E2+toy	-1	excluded	Threat or fear-aggression signal	Abrantes, 1997; Bradshaw et al., 2016
Growling	Freq	Toy	0	0	Not relevant for sociability or boldness scoring	-
Jumping	Freq	E1/E2	+1	excluded	Social engagement or play	See ethogram
Jumping	Freq	FD	+1	excluded	Social engagement or play	See ethogram
Jumping	Freq	Fence	-1	-1	Distress (escape)	See ethogram
Jumping	Freq	Toy	0	0	Not relevant for sociability or boldness scoring	-
Latency to approach	Lat		-1	-1	The longer it takes to approach, the more negative	
Licking	Dur	E1/E2	+1	excluded	Affiliative behavior	Abrantes, 1997
Licking	Dur	FD	+1	excluded	Affiliative behavior	Abrantes, 1997
Licking	Dur	Toy	0	+1	Curiosity	Abrantes, 1997
Lunge	Freq	E1/E2+toy	-1	-1	Sign of fear and anxiety	Loftus et al., 2012
Lunge	Freq	NO	-1	-1	Sign of fear and anxiety	Loftus et al., 2012
Lunge	Freq	Toy	0	0	Not relevant for sociability or boldness scoring	-
Mouthing	Dur	E1/E2	+1	excluded	Curiosity	Abrantes, 1997
Mouthing	Dur	FD	+1	excluded	Curiosity	Abrantes, 1997
Mouthing	Dur	NO	excluded	+1	Curiosity	Abrantes, 1997
Mouthing	Dur	Toy	excluded	+1	Curiosity	Abrantes, 1997
Nose /mouth licking	Freq		-1	-1	Stress or displacement signal	Abrantes, 1997; Bradshaw et al., 2016; Pastore et al., 2011

Pawing	Freq	E1/E2+toy	-1	excluded	Appeasment/pacifying or displacement; fear and anxiety	Abrantes, 1997; Bradshaw et al., 2016; Pastore et al., 2011
Pawing	Freq	FD	-1	excluded	Appeasment/pacifying or displacement; fear and anxiety	Abrantes, 1997; Bradshaw et al., 2016; Pastore et al., 2011
Pawing	Freq	NO	excluded	-1	Appeasment/pacifying or displacement; fear and anxiety	Abrantes, 1997; Bradshaw et al., 2016; Pastore et al., 2011
Pawing	Freq	Toy	0	-1	Appeasment/pacifying or displacement; fear and anxiety	Abrantes, 1997; Bradshaw et al., 2016; Pastore et al., 2011
Play	Dur	E1/E2+toy	+1	excluded	Social engagement	Abrantes, 1997
Risk assessment	Dur	E1/E2	-1	excluded	Hesitant/ambivalent approach; mild fear or caution	See ethogram
Risk assessment	Dur	E1/E2+toy	-1	excluded	Hesitant/ambivalent approach; mild fear or caution	See ethogram
Risk assessment	Dur	FD	-1	excluded	Hesitant/ambivalent approach; mild fear or caution	See ethogram
Risk assessment	Dur	NO	excluded	+1	Hesitant/ambivalent approach; mild fear or caution	See ethogram
Sniffing person/object	Dur	E1/E2	+1	excluded	Curiosity	Abrantes, 1997
Sniffing person/object	Dur	E1/E2+toy	+1	excluded	Curiosity	Abrantes, 1997
Sniffing person/object	Dur	FD	+1	excluded	Curiosity	Abrantes, 1997
Sniffing person/object	Dur	NO	excluded	+1	Curiosity	Abrantes, 1997
Sniffing person/object	Dur	Toy	0	+1	Curiosity	Abrantes, 1997
Sniffing the ground	Dur		0	0	Not relevant for sociability or boldness scoring	-
Stretching	Freq		0	0	Not relevant for sociability or boldness scoring	-
Tail between legs	Dur		-1	-1	Signal of fear and anxiety	Abrantes, 1997; Bradshaw et al., 2016; Schenkel, 1947
Tail wagging	Dur	E1/E2	+1	excluded	Communicative/positive arousal signal; affiliative or excited state	Abrantes, 1997; Bradshaw et al., 2016; Schenkel, 1947
Tail wagging	Dur	E1/E2+toy	+1	excluded	Communicative/positive arousal signal; affiliative or excited state	Abrantes, 1997; Bradshaw et al., 2016; Schenkel, 1947
Tail wagging	Dur	Fake dog	+1	excluded	Communicative/positive arousal signal; affiliative or excited state	Abrantes, 1997; Bradshaw et al., 2016; Schenkel, 1947
Tail wagging	Dur	Novel object	excluded	+1	Communicative/positive arousal signal; affiliative or excited state	Abrantes, 1997; Bradshaw et al., 2016; Schenkel, 1947
Tail wagging	Dur	toy	0	+1	Indicates exploratory engagement and environmental confidence	Abrantes, 1997; Bradshaw et al., 2016; Schenkel, 1947
Whining	Dur		-1	-1	Distress/submission/insecurity/fear signal	Abrantes, 1997; Loftus et al., 2012
Yawning	Freq		-1	-1	Displacement/pacifying behavior (stress)	Abrantes, 1997; Pastore et al., 2011

Table A2. Ethogram with definitions of the behaviors and instructions how to code them using BORIS, as well as modifiers the behavior is directed to. The term of 1 body length is referring to the body length of the puppy.

Category	Behavior	Definition	Coding	Variable	HA	FD	NO
Proximity	Close proximity	Time within 1 body length away from a person.	One paw gets within 1 body length of person/object until last paw leaves distance of 1 body length of person/object. Note: Close proximity is coded only towards person/object that is the closest to the pup. When another person/object comes within 1 body length, the proximity to previous one is finished and proximity towards new person/object begins.	Dur	E1/E2, E1/E2 +toy, door	FD, door	NO, door
	Latency to approach	Time from when the pup looks at the stimulus until the pup actively enters the area less than 1 body length from the stimulus.	Human Approach: Start when pup first orients head towards E1 when sits and looking for >1s to first getting within 1 body length from E1 (or first step towards E1 when E1 is already within 2 body lengths when first seeing it). If the pup never approaches, latency stops at the end of sitting sub-phase (when E1 grabs toy). Fake dog and Novel object: Start when pup first orients head towards FD/NO and looking for >1s to first getting within 1 body length from the fake dog/novel object (or first step towards FD/NO when pup is already within 2 body lengths when first seeing it).	Lat	E1/E2 Only during sitting phase	FD	NO
Tail	Tail wagging	The tail moves in different directions, in a relaxed manner, at a medium height (not rigid fast movements of the tip of the tail held upright, nor a small tail wagging with the tail held low, between the legs).	Start of first tail movement until tail being rigid.	Dur	E1/E2, E1/E2 +toy	FD, toy	NO, toy
Self-directed behaviors	Body shaking	Pup's whole body starts moving rapidly, from side to side while the pup stands.	Start of first movement.	Freq	any	any	any
	Stretching	The whole body is stretched in various ways: forelegs may be bent down while the pup's back is arched; hind legs may be straightened while the head is held up high.	Start of first movement.	Freq	any	any	any
	Yawning	The mouth is wide open, the neck is stretched.	Start of first movement.	Freq	any	any	any
	Nose/mouth licking	The mouth is slightly open, and the pup licks its upper lip or nose, on the right or on the left. Tongue visibly comes out of the mouth and moves across upper or lower lip.	Start of first movement.	Freq	any	any	any
Physical contact	Body contact	Pup touches or is touched by person or object with any parts of its body.	As soon as the bodies touch until they don't anymore.	Dur	E1/E2, E1/E2 +toy	FD, toy	NO, toy
	Climb on person	The pup puts the 2 front paws or climbs with all 4 paws on the person.	The moment in which the first 2 paws are on the person (any part of the human body).	Dur	E1/E2	-	-
	Jumping	Pup jumps on or towards person or object: both front paws off the ground, both hind paws on the ground, front of body higher than back part of body, movement vertical.	Highest point of movement.	Freq	E1/E2, toy, fence	FD, toy, fence	NO, toy, fence
	Licking	Pup using its tongue to touch the person or object.	As soon as tongue first touches person/object until tongue leaves the person/object at the end of a licking bout. New occurrence if >1s between licks.	Dur	E1/E2, toy	FD, toy	NO, toy
	Mouthing	Pup takes part of the person (also their clothes) or object into its mouth without aggression.	When mouth first touches person/clothes or object until release.	Dur	E1/E2, toy	FD, toy	NO, toy
	Sniffing person or object	Nose close to the person or object.	When nose gets within half a muzzle distance of person/object without other specific body movements, until head/nose gets more than half a muzzle distance away.	Dur	E1/E2, toy, E1/E2 +toy	FD, toy	NO, toy

	Genital sniffing	To sniff the genital area of the fake dog.	When nose gets within half a muzzle distance from the genital area of FD.	Freq	-	FD	-
	Pawing	Pup extends one paw towards person/object (distance less than 10 cm), the other is still on the ground. If the paw is extended towards the person/object with an attempt to grab the person/object or hold it in place, then this is not counted as pawing.	When the paw is at the highest point.	Freq	E1/E2, toy, E1/E2 +toy	FD, toy	NO, toy
	Carrying toy	Time spent moving around while carrying the toy.	Starts with first movement of the pup with the toy in his mouth until it is released and/or stops moving.	Dur	any	any	any
	Biting	The pup aggressively bites another subject or object in the skin and fur. Includes bite-shaking. Aggressively meaning other signs of aggression such as growling, teeth baring, lunging have been shown during/before.	The moment the mouth touches the person/object.	Freq	E1/E2, toy, E1/E2 +toy	FD, toy	NO, toy
Gazing	Gazing	Head oriented towards the stimulus.		Dur	H, E1/E2 Only when behind the fence	-	-
Vocalizations	Barking	Loud and short typical vocalization, which may be repetitive.	Begin of mouth movement until end, count as one bout if barks happen in direct succession. New bout if >1s break between barks.	Dur	E1/E2, E1/E2 +toy	FD, toy	NO, toy
	Growling	Actor snarls or growls at the specific receiver (only!) the actor's body posture being rigid. Mouth may be open, nose can be wrinkled.	New growl starts whenever there is >1s silence in between.	Freq	E1/E2, E1/E2 +toy	FD, toy	NO, toy
	Whining	The pup produces a high-pitched prolonged sound.	New bout if >1s break between whines.	Dur	any	any	any
Various	Play	Jumping around with wagging tail while looking at person or at object, play-bow (only with tail wagging, relaxed clumsy body posture).		Dur	E1/E2, E1/E2 +toy	FD	NO
	Lunge	Actor moves abruptly and rapidly towards recipient. Can but doesn't have to result in physical contact.		Freq	E1/E2, toy, E1/E2 +toy	FD. toy	NO, toy
	Tail between legs	Tail is between the hind legs or below the belly.		Dur	any	any	any
	Crouch	Lowered posture bending the legs, arching the back, lowered tail.	New crouch when main body went back to full height between.	Dur	E1	FD	NO
	Risk assessment	Back legs extended, the body weight is towards the front although the animal tries to be close to the stimulus with the front part of the body, the back part is extended; nose reaches towards object.		Dur	E1/E2, E1/E2 +toy	FD, toy	NO, toy
Activity	Activity level	See Table A2.1	Code it at the end of the test.	Scale	any	any	any
First reaction	First reaction	See Table A2.2	Code it at the end of the test.		E1/E2	FD	NO
Not visible	Not visible	Out of camera view.	Code whenever behavioral interactions are not codable due to low visibility. In this time, don't code anything else even if visible.	Dur	any	any	any
Disturbance	Disturbance	When behavior is clearly directed at what pups/other persons passing by/distracting activities by E1/E2 (e.g. feeding other dogs)/other dogs getting close enough to disturb the test.		Dur	any	any	any
Termination	Termination	Termination of test.	In the moment or termination.	Binary	any	any	any

Table A2.1 Definitions of the activity level of the puppy.

Give one individual score that represents the pup's activity level during the test	
Score	Description
1 – Inactive	The pup is either standing still, laying down quietly, or not moving at all. The pup does not want to move even with a lot of encouragement from the experimenter (avoidance to approach due to fear is not included here).
2 – Weakly active	The pup slowly moves parts of its body. The pup is walking slowly or needs a lot of encouragement from the experimenter to approach (avoidance to approach due to fear is not included here).
3 - Active	The pup moves its body. The pup is walking around or staying still in one place (not running) but approaches the experimenter/stimulus with just a little encouragement.
4 – Very active	The pup moves a lot. The pup is walking around with little running in between and approaches without hesitation when encouraged by the experimenter.
5 – Overactive	The pup runs around with little walking and approaches spontaneously (even without encouragement) the experimenter.

Table A2.2 Definitions of the puppies' first reaction to the stimulus.

First reaction in Human Approach (after E enters the fenced area), Fake Dog, and Novel Object Test		
MA	Avoidance – mild avoidance	After seeing stimulus, the pup steps to the side, gaze aversion, steps away, with other mild fear signals.
SA	Avoidance – strong avoidance	After seeing stimulus, the pup runs away while showing other fear signals, startle response.
FE	Approach – Fearful	Movement towards the stimulus with low tail (can be low tail wagging) and/or risk assessment (back legs extended, nose reaches towards object).
FR	Approach – Friendly	Movement towards the stimulus with midline or high relaxed tail wagging, relaxed posture.
RI	Approach – Rigid	Movement towards the stimulus with high tail position, no tail wagging or stiff tail wagging, stiff body posture.
AG	Approach – Aggressive	Movement towards the stimulus with signs of aggression: barking, biting, growling, showing teeth, snapping, lunging.
FRE	Freeze	After seeing stimulus, the pup does not move from the initial position and does not move its body.
UN	Uncertain	Response not possible to classify, because of external circumstances that made it impossible to compare it with the other pups or the pup does not show any reaction towards the stimulus.

Table A3. Model selection for parametric survival analyses (5- and 8-week predictors).

Model	Response	Predictor	df	AIC	ΔAIC	weight	LR X^2 (df)	p-value	n
Weibull	Survival 12w	Traits 8w	5	130.31	0.00	0.50	0.95 (3)	0.814	32
Log-logistic	Survival 12w	Traits 8w	5	130.33	0.02	0.50	0.73 (3)	0.866	32
Weibull	Survival 12w	Parasites 8w	4	258.88	128.57	0.00	0.33 (2)	0.847	46
Log-logistic	Survival 12w	Parasites 8w	4	258.97	128.66	0.00	0.50 (2)	0.778	46
Weibull	Survival 8w	Traits 5w	5	428.75	0.00	0.92	1.59 (3)	0.662	53
Log-logistic	Survival 8w	Traits 5w	5	433.52	4.77	0.08	1.92 (3)	0.588	53
Weibull	Survival 8w	Parasites 5w	4	655.32	226.57	0.00	4.29 (2)	0.117	87
Log-logistic	Survival 8w	Parasites 5w	4	663.15	234.40	0.00	4.47 (2)	0.107	87

Table A4. Time ratios (TR) from Weibull and log-logistic AFT survival models, predicting survival from 5-8 and 8-12 weeks using personality traits and parasite burden as predictors.

Model	Response	Predictor	Term	TR (95% CI)	p-value	n
Weibull	Survival 12w	Traits 8w	Boldness_8weeks	0.97 (-0.11 - 0.04)	0.372	32
Weibull	Survival 12w	Traits 8w	Soc_Hum_8weeks	1.00 (-0.03 - 0.04)	0.878	32
Weibull	Survival 12w	Traits 8w	Soc_Con_8weeks	1.02 (-0.05 - 0.09)	0.547	32
Log-logistic	Survival 12w	Traits 8w	Boldness_8weeks	0.97 (-0.11 - 0.05)	0.437	32
Log-logistic	Survival 12w	Traits 8w	Soc_Hum_8weeks	1.00 (-0.03 - 0.04)	0.884	32
Log-logistic	Survival 12w	Traits 8w	Soc_Con_8weeks	1.02 (-0.05 - 0.09)	0.575	32
Weibull	Survival 8w	Traits 5w	Boldness_5weeks	1.01 (-0.03 - 0.05)	0.774	53
Weibull	Survival 8w	Traits 5w	Soc_Hum_5weeks	1.00 (-0.02 - 0.03)	0.773	53
Weibull	Survival 8w	Traits 5w	Soc_Con_5weeks	0.98 (-0.06 - 0.01)	0.215	53
Log-logistic	Survival 8w	Traits 5w	Boldness_5weeks	1.00 (-0.05 - 0.05)	0.961	53
Log-logistic	Survival 8w	Traits 5w	Soc_Hum_5weeks	1.00 (-0.03 - 0.03)	0.936	53
Log-logistic	Survival 8w	Traits 5w	Soc_Con_5weeks	0.97 (-0.08 - 0.02)	0.196	53
Weibull	Survival 12w	Parasites 8w	N_fleas_8weeks	1.00 (-0.03 - 0.03)	0.799	46
Weibull	Survival 12w	Parasites 8w	N_ticks_8weeks	0.97 (-0.13 - 0.08)	0.620	46
Log-logistic	Survival 12w	Parasites 8w	N_fleas_8weeks	1.01 (-0.03 - 0.04)	0.709	46
Log-logistic	Survival 12w	Parasites 8w	N_ticks_8weeks	0.97 (-0.14 - 0.07)	0.540	46
Weibull	Survival 8w	Parasites 5w	N_fleas_5weeks	0.96 (-0.09 - 0.01)	0.111	87
Weibull	Survival 8w	Parasites 5w	N_ticks_5weeks	0.95 (-0.15 - 0.04)	0.285	87
Log-logistic	Survival 8w	Parasites 5w	N_fleas_5weeks	0.95 (-0.11 - 0.01)	0.073	87
Log-logistic	Survival 8w	Parasites 5w	N_ticks_5weeks	0.95 (-0.18 - 0.07)	0.393	87

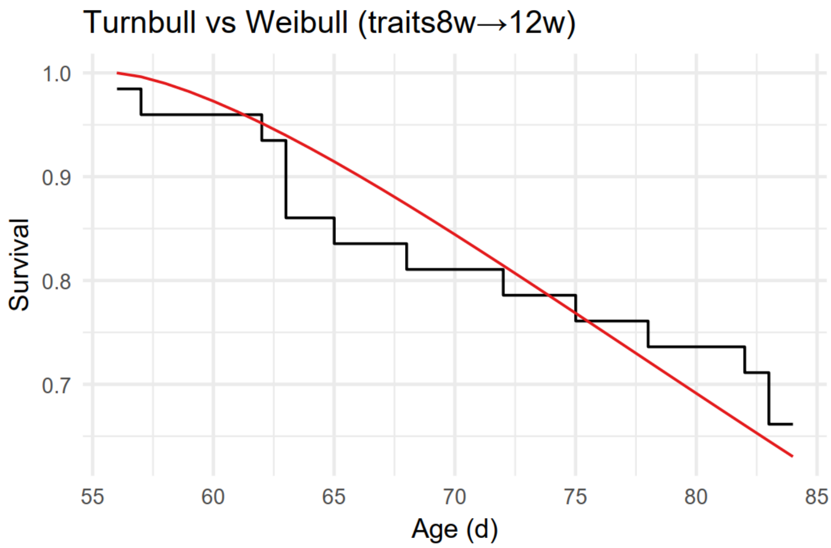

Figure A1. Non-parametric Turnbull step-function (black) vs. Weibull model curve (red) for puppies' survival to 12 weeks predicted by traits measured at 8 weeks.

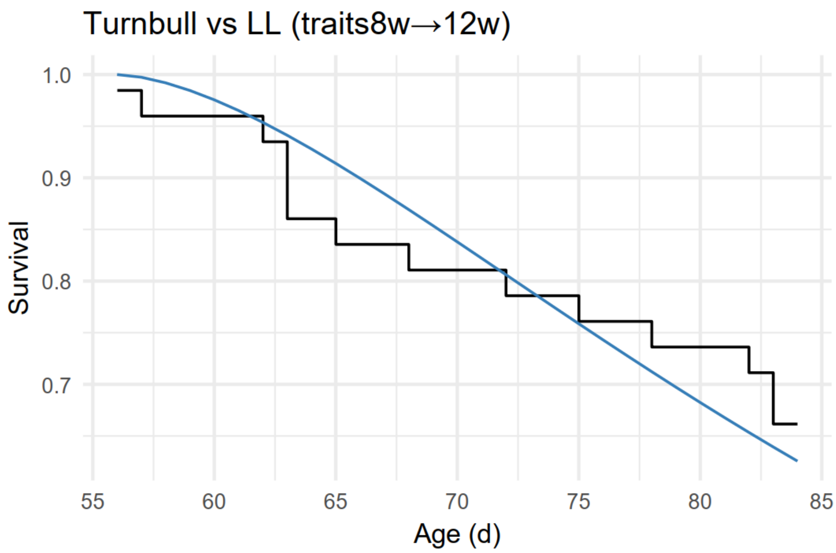

Figure A2. Non-parametric Turnbull step-function (black) vs. log-logistic curve (blue) for puppies' survival to 12 weeks predicted by traits measured at 8 weeks.

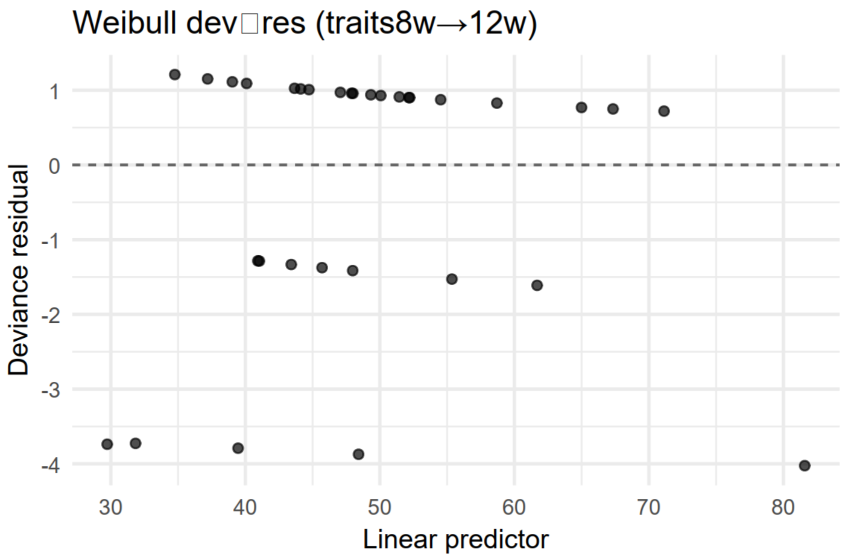

Figure A3. Deviance residual plot for Weibull model with personality traits at 8 weeks as predictor for survival to 12 weeks.

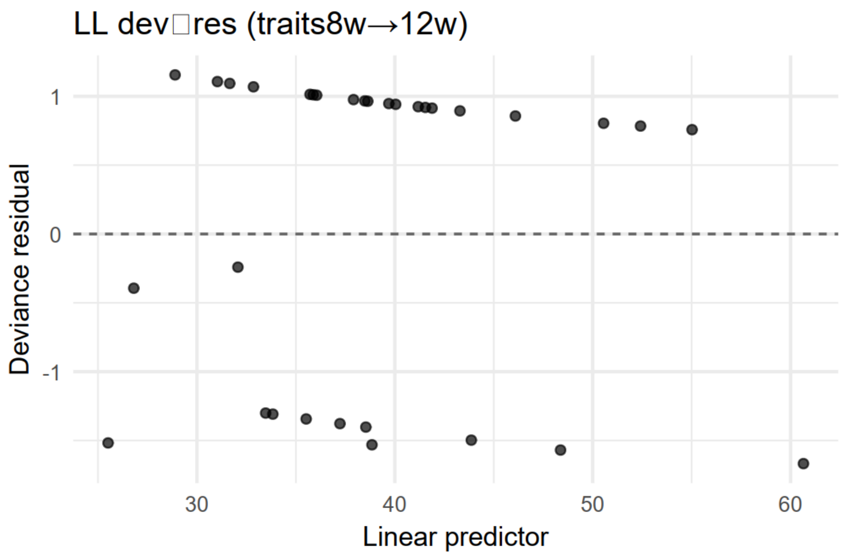

Figure A4. Deviance residual plot for log-logistic model with personality traits at 8 weeks as predictor for survival to 12 weeks.