

1 **Age influences domestic dog cognitive performance independent of average breed lifespan**

2 Marina M. Watowich¹, Evan L. MacLean^{2,3,4}, Brian Hare^{5,6}, Josep Call⁷, Juliane Kaminski⁸, Ádám Miklósi^{9,10}, Noah
3 Snyder-Mackler^{1,11,12,13,14,15}

4
5 **Correspondence:** Noah Snyder-Mackler, nsnyderm@asu.edu

6
7 ¹ Department of Biology, University of Washington, Seattle, WA 98195, USA

8 ² School of Anthropology, University of Arizona, Tucson, AZ 85719, USA

9 ³ Department of Psychology, University of Arizona, Tucson, AZ 85721, USA

10 ⁴ Cognitive Science, University of Arizona, Tucson, AZ 85721, USA

11 ⁵ Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, USA

12 ⁶ Center for Cognitive Neuroscience, Duke University, Durham, NC 27708, USA

13 ⁷ School of Psychology and Neuroscience, University of St Andrews, St Andrews, UK

14 ⁸ Centre for Comparative and Evolutionary Psychology, Department of Psychology, University of Portsmouth,
15 Portsmouth, UK

16 ⁹ Department of Ethology, Eötvös Loránd University, Budapest, Hungary

17 ¹⁰ MTA-ELTE Comparative Ethology Research Group, Budapest, Hungary

18 ¹¹ Center for Evolution & Medicine, Arizona State University, Tempe, AZ 85287, USA

19 ¹² School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

20 ¹³ Department of Psychology, University of Washington, Seattle, WA 98195, USA

21 ¹⁴ Nathan Shock Center of Excellence in the Basic Biology of Aging, Department of Pathology, University of
22 Washington, Seattle, WA 98195, USA

23 ¹⁵ Center for Studies in Demography and Ecology, University of Washington, Seattle, WA 98195, USA

24
25 **Abstract**

26 Across mammals, increased body size is positively associated with lifespan. However, within species, this
27 relationship is inverted. This is well illustrated in dogs (*Canis familiaris*), where larger dogs exhibit accelerated life
28 trajectories: growing faster and dying younger than smaller dogs. Similarly, some age-associated traits (e.g., growth
29 rate and physiological pace of aging) exhibit accelerated trajectories in larger breeds. Yet, it is unknown whether
30 cognitive performance also demonstrates an accelerated life course trajectory in larger dogs. Here, we measured
31 cognitive development and aging in a cross-sectional study of over 4000 dogs from 66 breeds using nine memory
32 and decision-making tasks performed by citizen scientists as part of the *Dognition* project. Specifically, we tested
33 whether cognitive traits follow a compressed (accelerated) trajectory in larger dogs, or the same trajectory for all
34 breeds, which would result in limited cognitive decline in larger breeds. We found that all breeds, regardless of size
35 or lifespan, tended to follow the same quadratic trajectory of cognitive aging—with a period of cognitive
36 development in early life and decline in later life. Taken together, our results suggest that cognitive performance
37 follows similar age-related trajectories across dog breeds, despite remarkable variation in developmental rates and
38 lifespan.

39
40 **Keywords**

41 Cognitive evolution, Cognitive aging, Breed differences, Citizen science, Executive function

42

43 **Introduction**

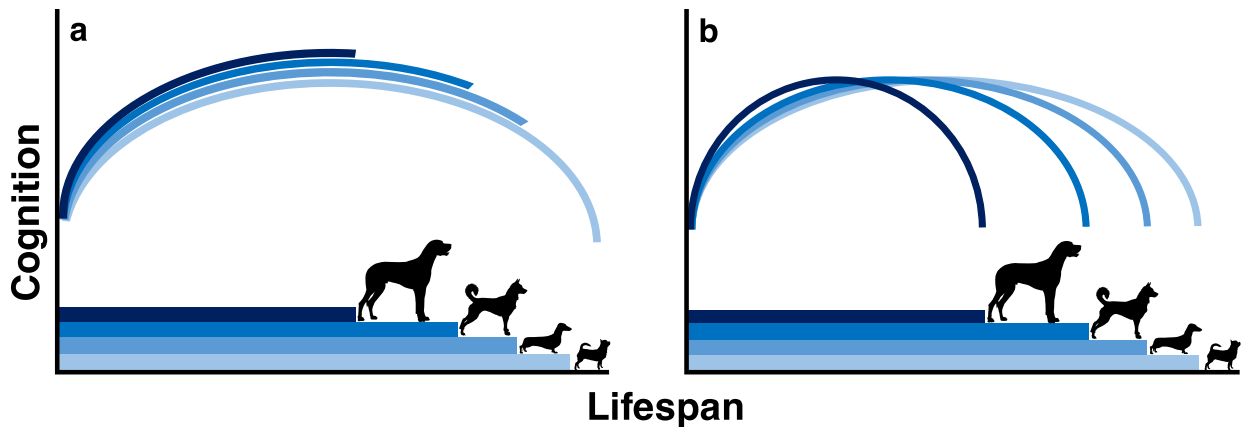
44 Across mammals, larger species tend to live longer than smaller species (Healy et al. 2014). Yet, within
45 species this pattern is reversed (Metcalf and Monaghan 2003; Austad 2010; Bartke 2017). This pattern is well-
46 documented in domestic dogs (Galis et al. 2007; Kraus et al. 2013; Fan et al. 2016) where larger dog breeds (e.g.,
47 Bernese Mountain Dog, mean lifespan = 7 years) have an expected lifespan that is approximately half that of smaller
48 breeds (e.g., Chihuahua, mean lifespan = 13 years; Jones et al. 2008). While large breeds take longer to mature than
49 small breeds, they weigh disproportionately more, and therefore have faster growth rates and an accelerated pace of
50 physiological aging (e.g., cellular damage; Fick et al. 2012; Kraus et al. 2013; Fan et al. 2016). Domestic dogs have
51 been under strong artificial selection for at least 15,000 years (vonHoldt et al. 2010), which has driven extensive
52 diversity in physical and life history traits (i.e., size, growth rate, lifespan). The large variation in these life history
53 traits, in particular, have made dogs an invaluable model species for studying the underpinnings of age-related
54 changes in health (Hoffman et al. 2018).

55 Domestic dogs also provide a powerful model in which to explore intraspecific patterns of cognitive aging.
56 In humans and other animals, including dogs, cognitive abilities, such as learning and memory, change throughout
57 aging (Craik and Bialystok 2006; Bizon and Woods 2009; Harada et al. 2013; Chapagain et al. 2018). However, for
58 some cognitive processes, dogs may even provide a better model for human cognition than rodents and nonhuman
59 primates, potentially due to convergent evolution between humans and dogs (Miklósi et al. 2004; Hare and
60 Tomasello 2005; Hare 2017; MacLean et al. 2017). For millennia, humans have selected dogs for both behavioral
61 (i.e., herding, hunting) and physical traits (Ostrander et al. 2017; Parker et al. 2017), contributing to the extensive
62 diversity seen across modern breeds. While the association between domestic dog cognition and other life history
63 traits (e.g., age) remains largely unexplored, there is evidence that absolute brain size is associated with breed
64 differences in executive function (Horschler et al. 2019) – a cognitive domain responsible for inhibitory control,
65 mental flexibility, and decision-making (Alvarez and Emory 2006; Jurado and Rosselli 2007).

66 Executive functions typically include inhibition (i.e., self-control and selective memory), working memory,
67 and cognitive flexibility (Diamond 2013). In humans, executive function, learning, and long-term memory have
68 largely been found to increase in early life and decrease in late life (Craik and Bialystok 2006; Harada et al. 2013;
69 but see Verhaeghen 2011). Other cognitive abilities (e.g., vocabulary and general knowledge) increase steadily
70 throughout life (i.e., linearly) or increase rapidly and then plateau (i.e., resembling a positive logarithmic curve)

71 (Harada et al. 2013). Similar to humans, domestic dogs experience changes to critical cognitive functions across life
72 (Chapagain et al. 2018). Recent studies from laboratory and pet dogs have demonstrated that learning, memory, and
73 cognitive functions under executive control decrease in older dogs (Adams et al. 2000; Tapp et al. 2003; Szabó et al.
74 2016; Wallis et al. 2016). Older dogs also show greater variability in the extent of cognitive decline with age
75 (Adams et al. 2000). One source of this variability may be lifelong behavioral training, which has been associated
76 with greater sustained and selective attention in older dogs (Chapagain et al. 2017). Although domestic dogs exhibit
77 age-related cognitive changes, we still know very little about how cognition changes with age, in large part due to
78 sample size: collecting data from enough very young and very old dogs has been challenging (Szabó et al. 2016). To
79 date, most studies of dog cognitive aging have focused on one breed or a small number of breeds, which, due to the
80 limited variability in life history within individual breeds, has limited our ability to examine associations between
81 cognitive aging and physiological pace of aging. Consequently, the extent to which cognitive changes throughout
82 aging are associated with life history traits that covary with physiological pace of aging (as measured by average
83 breed lifespan) remains unknown.

84 Here, we investigated the associations between lifespan and cognitive traits in dogs, in order to test the
85 hypothesis that animals with faster life histories also exhibit earlier onset of and/or more rapid cognitive decline. We
86 addressed two questions using a cross-sectional dataset of more than 4,000 dogs from 66 breeds collected from
87 participants of the Dognition project, a citizen-science initiative in which owners perform simple cognitive tests with
88 their dogs at home (Stewart et al. 2015). First, we tested how cognition changes across the lifespan of domestic
89 dogs. To date, many studies of dog cognition have modeled cognition as a linear process throughout the lifespan, yet
90 data from humans, apes, and several within-breed studies of domestic dogs suggest the likelihood of non-linear
91 changes across development and senescence (Craik and Bialystok 2006; Harada et al. 2013; Wallis et al. 2014;
92 Manrique and Call 2015). Second, we tested if and how a key life history trait, expected breed lifespan, affected the
93 trajectory of cognition across the lifespan. We explicitly tested two alternative hypotheses: i) *truncation*: that all
94 breeds have similar cognitive trajectories throughout aging with larger breeds having a limited period of cognitive
95 decline (Fig. 1a), and ii) *compression*: that changes in cognitive abilities scale with lifespan such that larger dogs
96 have a compressed (i.e., accelerated) cognitive trajectory (Fig. 1b).



98 **Fig. 1 Alternative models of cognitive aging in dogs. a** Schematic of the truncation hypothesis in which larger and
 99 smaller dog breeds have similar cognitive trajectories throughout aging. Under this hypothesis, large dog breeds
 100 experience limited cognitive decline because they typically die before the more precipitous cognitive decline
 101 experienced by longer-lived, smaller breeds. **b** The compression hypothesis in which cognitive performance scales
 102 with lifespan, such that larger breeds will have an accelerated cognitive trajectory.

103

104 **Methods**

105 **Data sources**

106 Cognitive performance data were collected from *Dognition.com*, a citizen science website which provides
 107 users with video instructions for completing simple cognitive experiments at home with their dogs. Owners entered
 108 data into the website by answering simple questions about their dog's behavior during the cognitive tests (e.g.,
 109 which location did your dog approach?). Importantly, results from citizen scientists using Dognition recapitulate
 110 results from professional scientists working in controlled laboratory settings (Stewart et al. 2015). Here, we
 111 restricted our analysis to data collected prior to April 2018 from purebred dogs with known sex, age, reproductive
 112 alteration status (i.e., spayed/neutered vs. intact), and breed (n= 4,419). Dogs in the study represented 66 breeds and
 113 ranged in age from < 1 to 14.2 years with a mean age of 4.78 years (standard deviation \pm 3.13; Supplemental Fig. 1).
 114 To ensure representative sampling, only breeds with 10 or more individuals were retained for analysis
 115 (Supplemental Table 1). We used data from purebred dogs to ensure that we could estimate mean breed lifespan and
 116 to control for relatedness among breeds based on breed-averaged genotypic data (Parker et al. 2017; Supplemental
 117 Table 2). We used estimates of mean breed lifespan from Jones et al. (2008; Supplemental Table 3). Because recent

118 studies have found behavioral modifications correlated with reproductive alteration (Hart 2001; Mongillo et al.
 119 2017; Scandurra et al. 2019), we also included reproductive alteration status as a covariate in all models.

120 We included data from nine cognitive tasks measuring diverse processes involving aspects of executive
 121 function, such as memory, reasoning, decision making, self-control, as well as measures of social cognition (Stewart
 122 et al. 2015; Horschler et al. 2019; Table 1). Sample size varied across tasks due to participant attrition across the
 123 series of experiments. We focused our analyses on tasks involving executive function as it is one of the cognitive
 124 domains most susceptible to effects of aging (Jurado and Rosselli 2007). Seven of the Dognition tasks involved an
 125 object-choice paradigm in which the dog had to choose one of two possible options, across a series of trials
 126 (range=1-6, mode=4; Table 1). One of the other two tasks was the eye contact task, in which the owner held a piece
 127 of food up to their face and recorded the time until the dog broke eye contact (up to 90 seconds). This task was
 128 designed as a measure of dog’s social engagement. In the remaining task, the owner set a treat before the dog,
 129 instructed the dog not to take a treat, and recorded the time until the dog took the treat (up to 90 seconds) while the
 130 owner i) was visibly watching the dog, ii) had their back turned to the dog, or iii) faced the dog with their eyes
 131 closed (detailed in Stewart et al. 2015). Although originally developed as a measure of social cognition (sensitivity
 132 to cues about the human’s visual perspective), recent analyses have focused on the executive function component of
 133 this task, which requires dogs to delay gratification (Horschler et al. 2019). Following this approach, we considered
 134 the latency to take the forbidden treat as a measure of executive function in our analyses. To summarize
 135 performance in this task, we performed a principal component analysis on the latencies to take the treat across
 136 conditions. This analysis yielded one principal component which explained 88% of the variance and is subsequently
 137 referred to as ‘delay of gratification’. The Dognition battery also includes a contagious yawning task which we did
 138 not include because preliminary analyses showed minimal evidence for contagious yawning in this sample.

139

140 **Table 1** Description of cognitive tasks, cognitive processes the task was designed to test, number of trials conducted
 141 per task, number of individuals included in analysis, and number of breeds included in analysis

| Task | Description | Cognitive processes | Trials | Total dogs | Total breeds |
|-------------|---|---------------------|--------|------------|--------------|
| Eye contact | The owner holds a treat to their face and records if and when the dog breaks eye contact within 90 seconds. | Social engagement | 3 | 4359 | 65 |

| | | | | | |
|------------------------|---|--|---|------|----|
| Arm pointing | The owner places one treat to their right and left, points to one treat location, and records the location the dog first approaches. | Social cognition/ communication | 6 | 4367 | 65 |
| Foot pointing | The owner places one treat to their right and left, extends their foot toward one treat location, and records the location the dog first approaches. | Social cognition/ communication | 6 | 4071 | 63 |
| Delay of gratification | | Inhibition/self-control | 6 | 2826 | 51 |
| Watching condition | The owner places the treat in front of the dog and verbally commands the dog not to take the treat. The owner records the duration of time until the dog takes the treat, up to 90 seconds. | | 2 | 2826 | 51 |
| Closed eyes condition | Same as above, with the owner closing their eyes. | | 2 | 2826 | 51 |
| Turned back condition | Same as above, with the owner turning their back. | | 2 | 2826 | 51 |
| Memory vs. pointing | In view of the dog, the owner places a treat under one of two cups, then proceeds to point to the other cup. The owner records which location the dog first approaches. | Bias for information from memory vs. communication | 6 | 2346 | 48 |
| Memory vs. smell | Allowing the dog to see, the owner places a treat under one of two cups, then blocks the dog's view while switching the position of the treat. The owner records which location the dog first approaches. | Bias for information from memory vs. olfaction | 4 | 2187 | 47 |
| Delayed memory | In full view of the dog, the owner places a treat under one of two cups and then waits 60, 90, 120, and 150 seconds (across four trials) before releasing the dog. Then the owner records which location the dog first approaches. | Short-term memory/ sustained attention | 4 | 2124 | 47 |
| Inferential reasoning | The owner appears to place treats under two cups, while only baiting one. The owner raises the empty cup to show it is empty and records which location the dog first approaches. | Inferential reasoning/ reasoning by exclusion | 4 | 1737 | 42 |
| Physical reasoning | Blocking the dog's view, the owner places two pieces of folded paper on the floor. The owner places a treat under one paper so that the paper is elevated by the treat while the other paper is flat and records which location the dog first approaches. | Physical causality/ inferential reasoning | 4 | 1654 | 40 |

142

143 **Statistical Analysis**

144 To address the questions of i) how cognitive performance changes across domestic dog lifespan (Equations
145 1, 2, and 3) and ii) whether cognition scales with mean breed lifespan (Equations 3 and 4), we compared the fit of all
146 four mixed effects models for each of the seven tasks with a binomial response and ii) the two linear response
147 variables (eye contact and the principal component scores reflecting delay of gratification; Supplemental Tables 4,
148 5). Because many cognitive abilities in humans exhibit a negative quadratic relationship (an inverted U-shape) with
149 age (in particular those associated with executive processes), while others tend to increase throughout life or
150 increase quickly during development and then plateau (Craik and Bialystok 2006; Harada et al. 2013; Wallis et al.
151 2014), we tested if cognitive performance followed these trajectories by modeling age as a quadratic, linear, and
152 logarithmic predictor (Supplemental Table 4).

153 (1) **Linear trajectory:** *Cognitive measure* ~ *sex* + *reproductive alteration* + *age* + *mean breed lifespan*

(2) **Logarithmic trajectory:** *Cognitive measure* ~ *sex* + *reproductive alteration* + $\log(\text{age})$ +
mean breed lifespan

(3) **Quadratic trajectory (additive):** *Cognitive measure* ~ *sex* + *reproductive alteration* + *age* + age^2 +
mean breed lifespan

(4) **Quadratic trajectory (interactive):** *Cognitive measure* ~ *sex* + *reproductive alteration* +
 $\text{age} \times \text{mean breed lifespan}$ + $\text{age}^2 \times \text{mean breed lifespan}$

154 **Equations 1, 2, 3, and 4** Equations 1, 2, and 3 represent hypothesized trajectories of cognitive aging, based on
155 previously described patterns of cognitive aging. Equations 3 and 4 represent the truncation and compression
156 hypotheses
157

158 In all models, the age and mean breed lifespan predictors were mean centered and scaled to a standard
159 deviation of one. Age and mean breed lifespan were in units of years and therefore one order of magnitude larger
160 than the predictors of sex and reproductive alteration. Scaling the predictors of age and mean breed lifespan made
161 them similar in magnitude to the predictors of sex and reproductive alteration, facilitating interpretation of the model
162 results (Harrison et al. 2018). All models of the quadratic trajectory included orthogonal linear and quadratic
163 predictors of age. Mixed-effects models of the seven binomial measures were carried out using the ‘PQLseq’
164 package, which implements the mixed modeling framework MACAU in the R environment (Lea et al. 2015; Sun et
165 al. 2019). This allowed us to model a binomial outcome variable (i.e., number of times dog chose the left cup out of
166 6) while controlling for background genetic similarity among the breeds, which was calculated from a recent
167 genomic analysis of 150,067 SNPs in 1,346 dogs representing 161 breeds (Parker et al. 2017; Supplemental Table
168 2). The eye contact and delay of gratification measures were modeled controlling for breed relatedness using the

169 ‘EMMREML’ package (Akdemir and Okeke 2015) in the R environment. Only breeds for which we had both
170 cognitive and genetic data were included in our analyses (Supplemental Table 1). Model fits were compared using
171 Akaike information criterion (AIC; Akaike 1974). To test the sensitivity of our models, we also repeated these
172 analyses excluding overrepresented breeds, which were breeds which each constituted over 5% of the dataset
173 (Supplemental Table 6). Five breeds fit this criterion (Australian Shepherds, Border Collies, German Shepherd
174 Dogs, Golden Retrievers, and Labrador Retrievers) and together comprised over 45% of the dataset. For models of
175 the three tasks involving gesture following (arm pointing, foot pointing, and memory vs. pointing), we included
176 behavioral training history as a predictor in the truncation and compression models to ensure that our results were
177 not confounded by the correlation between dog size and training history (training history was rated on a scale of 1
178 [none] – 4 [substantial]; $r_s = 0.12$, $p < 0.001$; Supplemental Table 7; Horschler et al. 2019).

179

180 **Delayed memory task**

181 We considered the delayed memory task the clearest test of basic memory because other tests involving
182 memory measured preferences and biases, where memory was pitted against other information sources (e.g.,
183 memory of treat location vs. owner’s pointing, memory of treat location vs. scent of the treat). Although designed
184 and interpreted as a measure of memory, it is possible that the delayed memory task also reflects variation in
185 sustained attention, since the hiding locations were not out of the dog’s view during the delay. However, unlike
186 traditional sustained attention tasks, there was no cue provided at the end of the delay, and thus subjects would most
187 likely have been reliant on memory to motivate their search for food at the baited location. We modeled all trials
188 from this task to test the truncation and compression hypotheses, however, we focused our analyses on the 150
189 second trial as this trial was the longest time delay and likely the most cognitively challenging. Importantly, the
190 results of the 60, 90, and 120 second delayed memory trials were very similar to the 150 second trial (Supplemental
191 Table 8).

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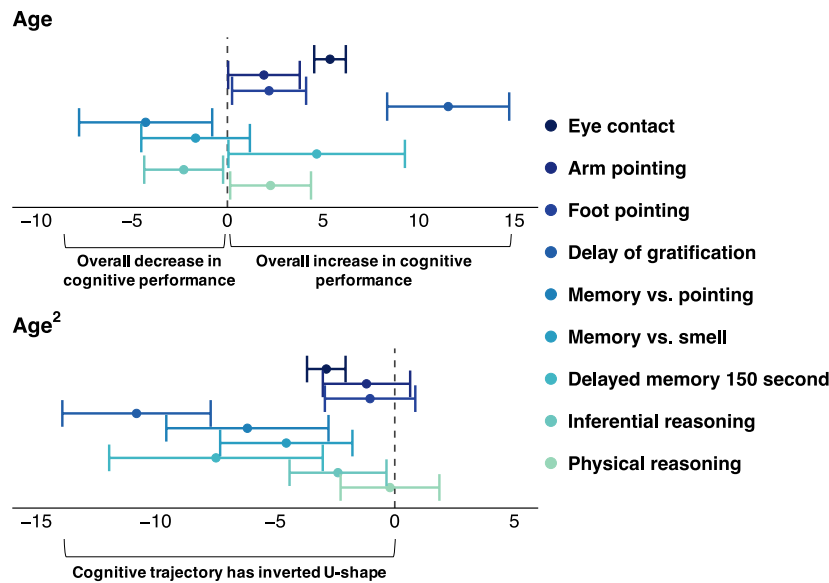
193 **Results**

194 **Cognition across the lifespan**

195 For all tasks, the best models ($\Delta AIC > 2$) included the quadratic predictor of age, compared to linear or
196 logarithmic, meaning that cognitive performance followed the expected inverted U-shaped trajectory – increasing in

197 early life and declining in late life (Figs. 2, 3; Supplemental Fig. 2; Supplemental Table 4). Although the best
 198 models included quadratic functions of age, the coefficient for the quadratic term was significant in only six tasks
 199 (eye contact, delayed memory, memory vs. pointing, memory vs. smell, and inferential reasoning tasks, as well as
 200 the delay of gratification score; Fig. 2, Fig. 3; Supplemental Tables 4, 5, 8). Models without a significant age² term
 201 (arm pointing, foot pointing, and physical reasoning tasks) showed an increase in cognitive performance throughout
 202 aging (Supplemental Table 5).

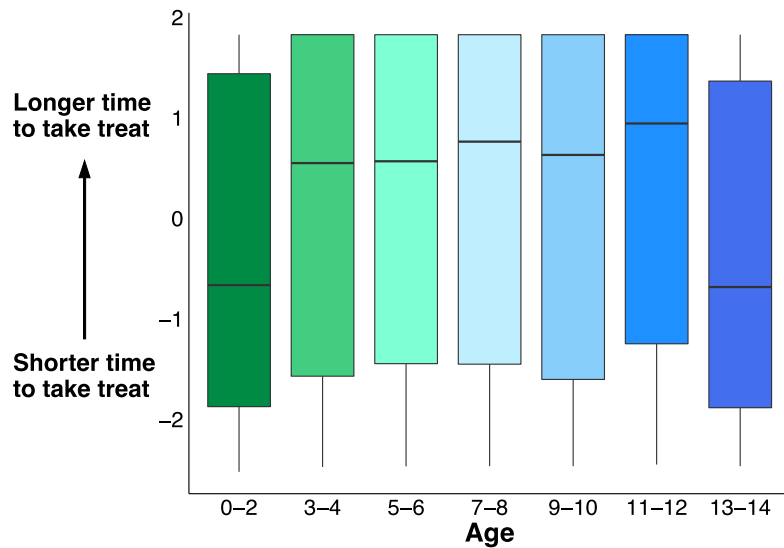
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205 **Fig. 2 Age has both linear and quadratic associations with cognitive function.** Effect sizes and estimated
 206 confidence intervals ($beta \pm 1.96 \times SE$) of age and age² predictor variables for the additive (truncation) models for
 207 each cognitive task. Estimated confidence intervals that do not cross the line of null effect ($x = 0$) are statistically
 208 significant. For ease of interpretation and visualization, and to keep all variables on a similar scale, we converted the
 209 beta for the eye contact task to minutes

210



211

212 **Fig. 3 Self-control changes with age.** Delay of gratification principal component 1 values for 2-year age groups.

213 The delay of gratification task measures the time until the dog takes a treat (latency) under conditions of the owner

214 watching, closing their eyes, and turning their back. Increasing y-axis values indicate greater performance in

215 prolonging gratification (i.e., increased latency to take the treat)

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217 **Truncation vs. compression models**

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Models testing the truncation hypothesis fit the data better than or as well as models of the compression hypothesis for seven of the nine tasks (Table 2; Supplemental Table 5). The two tasks for which the model of the compression hypothesis had a better model fit were the eye contact task and delay of gratification score. However, neither of these models had significant interactions with mean breed lifespan, between age and mean breed lifespan, or between age² and mean breed lifespan. For models of the compression hypothesis, only the arm pointing ($\beta = 2.196$, SE = 0.996, $p = 0.027$, $n = 4367$) and foot pointing tasks ($\beta = 2.017$, SE = 1.028, $p = 0.049$, $n = 4071$) showed significant interaction effects between age² and mean breed lifespan, while the memory vs. pointing task ($\beta = 0.087$, SE = 0.042, $p = 0.037$, $n = 2346$) had a significant effect of mean breed lifespan in models of the truncation and compression hypotheses. These associations would support the compression hypothesis; however, interactive models of these tasks did not fit the data better than additive models representing the truncation hypothesis ($\Delta AIC < 2$; Table 2; Supplemental Table 5). Our sensitivity analyses that excluded overrepresented breeds generally recapitulated results of the comparison between truncation and compression hypothesis models (Supplemental Table 6). In these analyses, fewer tasks had significant effects of age and age², likely due to reduced power, however the

231 results were very similar to analyses with the entire dataset and did not suggest that our results were being driven by
 232 breeds that were overrepresented in the data. While we focused our analyses on the 150 second delayed memory
 233 trial, we evaluated how age affected cognitive performance across all delayed memory trials by modeling delay-
 234 specific accuracies in young (0-5 years), middle-aged (6-10 years), and old dogs (11+ years). Comparing the slope
 235 of the delay function, we found that dogs 11 years and older performed lower across all delayed memory trials
 236 (Supplemental Fig. 3).

237

238 **Table 2** Comparing the fit of models of the truncation hypothesis and the compression hypothesis for each cognitive
 239 task. Lower AIC value indicates a better model fit. $\Delta AIC > 2$ is considered a difference in model fit. The numbers in
 240 bold denote a difference in model fit between truncation and compression models

| Task | ΔAIC of truncation hypothesis models and compression hypothesis models (compression – truncation) | Model with better fit |
|---------------------------|---|------------------------|
| Eye contact | -13.0 | compression hypothesis |
| Arm pointing | 1.2 | no difference |
| Foot pointing | -0.3 | no difference |
| Delay of gratification | -7.5 | compression hypothesis |
| Memory vs. pointing | 0.1 | no difference |
| Memory vs. smell | 0.8 | no difference |
| Delayed memory 150 second | -0.2 | no difference |
| Inferential reasoning | 2.4 | truncation hypothesis |
| Physical reasoning | 1.7 | no difference |

241

242 **Gesture following**

243 We observed associations between predictors involving breed-mean lifespan for the three tasks involving
 244 gesture following (arm pointing, foot pointing, and memory vs. pointing), supporting the compression hypothesis,
 245 although model fit did not differ substantially between models of the truncation and compression hypothesis.
 246 Additionally, in all models of gesture following, the age coefficient indicated increases in performance with aging,
 247 rather than late-life deterioration of cognitive performance, suggesting that these associations are not likely to
 248 support accelerated cognitive deterioration in faster-aging breeds. To ensure that our results were not confounded by
 249 the correlation between dog size and training history, we included training as a predictor in the truncation and
 250 compression models for all gesture following models. The proportion of dogs in each category of training history
 251 was similar between intact and spayed and neutered individuals, males and females, and across dogs of all ages (in
 252 one-year age groups). Effects of breed lifespan were reduced to statistically indistinguishable from zero when we

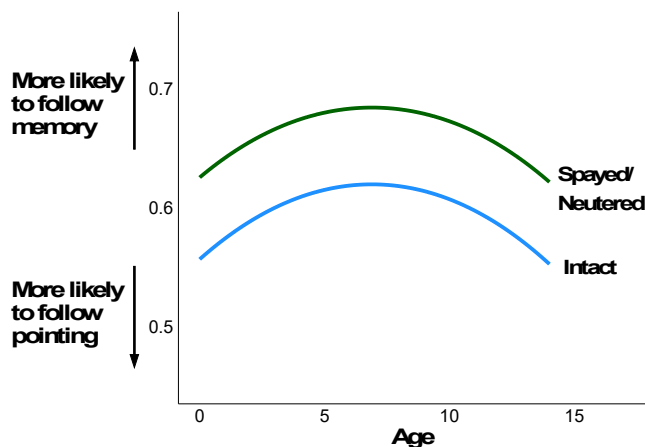
253 included training history in the models of gesture following tasks (arm pointing [$mean\ breed\ lifespan \times age^2$]: β
254 = -0.64, SE = 0.915, $p = 0.485$, $n = 1105$; foot pointing [$mean\ breed\ lifespan \times age^2$]: $\beta = 0.275$, SE = 0.936, $p =$
255 0.769, $n = 1057$; memory vs. pointing [mean breed lifespan]: $\beta = 0.071$, SE = 0.083, $p = 0.394$ $n = 720$;
256 Supplemental Table 7). However, because not all owners reported their dog's training history – resulting in reduced
257 power for this analysis – we could not rule out the possibility that this reduction in significance was due to a smaller
258 sample size. We therefore compared this analysis to an analysis of the same subsample excluding training history as
259 a predictor (Supplemental Table 7) and found that the effects of mean breed lifespan were not significant.

260

261 Associations of reproductive alteration vary across gesture following tasks

262 Reproductive alteration was associated with decreased gesture following throughout aging (Fig. 4; arm
263 pointing: $\beta = -0.117$, SE = 0.039, $p < 0.01$, $n = 4367$; memory vs. pointing: $\beta = 0.379$, SE = 0.097, $p < 0.001$, $n =$
264 2346; Supplemental Table 5). After controlling for training history in analyses of the arm pointing and memory vs.
265 pointing tasks, reproductive alteration was still significantly associated with decreased gesture following (arm
266 pointing: $\beta = -0.272$, SE = 0.073, $p < 0.001$, $n = 1105$; memory vs. pointing: $\beta = 0.527$, SE = 0.164, $p < 0.01$, $n =$
267 720), indicating that spayed or neutered animals were less likely to follow social cues from their owner, even after
268 controlling for training history (Supplemental Table 7).

269



270

271 **Fig. 4 Gesture following differs between intact and spayed and neutered dogs.** Predicted cognitive trajectory for
272 the memory vs. pointing task throughout aging (years) of an average dog in the dataset whether spayed or neutered
273 (green) or intact (blue), with bootstrapped 95% confidence intervals

274

275 **Sex differences**

276 In the eye contact task, males maintained eye contact with the experimenter longer than females ($\beta = 2.26$,
277 $SE = 0.738$, $p = 0.002$, $n = 4359$), but this effect size was small (males held eye contact for an average of 2.26
278 seconds longer than females). In the delayed memory task, males were more likely than females to locate a treat
279 after the 150 second delayed memory trial ($\beta = 0.204$, $SE = 0.101$, $p = 0.043$, $n = 2124$), but not any other delayed
280 memory trial; again this effect was small, but statistically significant (males had 22% higher odds of choosing the
281 cup with the treat). After performing our sensitivity analyses by excluding overrepresented breeds, males still
282 showed longer social engagement in the eye contact task ($\beta = 2.323$, $SE = 1.008$, $p = 0.021$, $n = 2318$) but sex
283 differences for the 150 second delayed memory trial were no longer significant.

284

285 **Discussion**

286 We investigated age-related changes in dog cognition and found that all cognitive measures changed across
287 the lifespan, with most measures following a clear negative quadratic trajectory across the lifespan. For each of the
288 nine cognitive tasks we evaluated, models with a quadratic term for age better fit the data than linear and logarithmic
289 terms and six of these cognitive tasks showed a distinct inverted U-shape across aging (Fig. 2; Supplemental Fig. 2;
290 Supplemental Tables 4, 5), indicating that a broad suite of cognitive processes in domestic dogs increase in early
291 life, peak in midlife, and decrease in late life. Additionally, we found that cognitive performance in tasks testing
292 physical reasoning and the propensity to follow owners' pointing gestures (without competing sources of
293 information) increase throughout aging.

294 Tasks directly testing memory and self-control were the clearest tests of executive function and had
295 particularly robust quadratic curves throughout aging (Fig. 2.; Fig. 3.; Supplemental Table 5). In humans, executive
296 function follows a similar negative quadratic trajectory throughout the lifespan and is one of the cognitive domains
297 most susceptible to aging. Declines in executive function greatly impact daily life by reducing cognitive
298 performance in domains such as decision making, memory, and self-control (Jurado and Rosselli 2007; Alvarez and
299 Emory 2006; Bizon and Woods 2009; Harada et al. 2013). Similar declines have been reported in nonhuman primate
300 and rodent models (Moore et al. 2006; Rodefer and Nguyen 2008; Beas et al. 2013), and recently described for
301 domestic dog attention (Wallis et al. 2014). Our findings extend these similarities to dogs across a range of cognitive

302 processes, thus building on previous laboratory work with dogs (Milgram et al. 1994; Head et al. 2001; Tapp et al.
303 2003) and advancing companion dogs as a useful model for human cognitive aging.

304 To assess associations between cognition and aging, we tested models representing what we have termed
305 the ‘truncation hypothesis’, in which all dogs have similar cognitive trajectories, and the ‘compression hypothesis’,
306 in which the timing of decline is accelerated in shorter-lived breeds. Models representing the truncation hypothesis
307 fit the data better than or as well as models representing the compression hypothesis across seven of the nine
308 cognitive tasks (Table 2; Supplemental Table 5). The two tasks for which models representing the compression
309 hypothesis fit the data better than models representing the truncation hypothesis did not have significant associations
310 of mean breed lifespan or between mean breed lifespan and linear or quadratic terms of age. Additionally, all models
311 representing the compression hypothesis lacked significant interactions between age and mean breed lifespan after
312 controlling for training history. Thus, we conclude that there is not sufficient evidence for the compression
313 hypothesis, and that these results most strongly support the truncation hypothesis. Together, our results suggest that
314 all dog breeds, regardless of average breed lifespan or rate of physiological aging, exhibit similar cognitive aging
315 trajectories such that larger dogs may experience a limited cognitive decline at the end of their shorter lives.

316 Although the pace of physiological aging varies with lifespan, there is evidence that the age of onset of
317 senescence does not differ among breeds, except, perhaps, in very large breeds (Kraus et al. 2013). If general onset
318 of senescence is similar among breeds, larger breeds will tend to have an abnormally shortened senior period, while
319 smaller breeds will likely undergo a protracted decline. Our findings indicate a similar pattern in cognitive
320 performance and are concordant with recent work finding similar prevalence of canine dementia across breeds of
321 varying size (Salvin et al. 2010, 2012). However, Kraus et al. (2013) suggest that large breeds physiologically
322 deteriorate rapidly, which we did not detect for cognitive aging. Together, these results may suggest that the
323 pathways which influence cognitive aging may be partially decoupled from those which affect the pace of
324 physiological aging. While further investigation is clearly warranted, these findings have important implications for
325 dog owners considering the quality of life during the senior period in terms of both cognitive and physiological
326 health.

327 We also observed effects of reproductive alteration on tasks involving responses to pointing gestures. Intact
328 dogs were more likely than spayed and neutered dogs to follow owners’ cues across two tasks involving arm
329 pointing even after controlling for training history (Supplemental Table 7). These findings are consistent with results

330 from a recent study that demonstrated reduced tendency of gonadectomized female dogs to follow human pointing
331 gestures compared to intact females (Scandurra et al. 2019). Neutering increases food motivation and decreases
332 metabolic rate, which can lead to lower energy levels and increased risk of obesity (Duffy and Serpell 2006; German
333 2006). It is therefore possible that neutered dogs had a greater motivation to obtain the food than intact dogs and
334 were less attentive to the cue given by the owner. It is unclear how sex hormones alter cognition and behavior in
335 dogs, however, there is some evidence that intact male dogs may exhibit slower cognitive decline than neutered
336 males (Hart 2001) which may be due to neuroprotective activity of sex hormones (Zárate et al. 2017). Additionally,
337 our findings demonstrated few and inconsistent sex-related differences in cognitive performance. Sex was
338 significantly associated with performance on two measures, duration of eye contact, in which male dogs held
339 slightly longer eye contact than females, and the 150 second delayed memory trial, in which males had a greater
340 propensity than females to remember treat location after this time delay (although this effect was not detected for the
341 sensitivity analyses with reduced sample size). Sex differences in dog cognition have been reported across a variety
342 of measures including looking times in violation of expectation tasks, gaze at human faces following oxytocin
343 administration, and speed and accuracy in spatial memory tasks (Müller et al. 2011; Nagasawa et al. 2015; Mongillo
344 et al. 2017). However, these studies found that female dogs tended to show longer looking times compared to
345 males, and better performance on spatial memory, effects in the opposite direction to those we observed. Given the
346 inconsistency across studies, it will be important for future research to assess the robustness of sex differences on
347 these measures, as well as specific factors that may determine the nature of these effects (Miller and Halpern 2014).

348 One limitation of this study stems from a lack of very old dogs in our sample. We had relatively few dogs
349 of very old age: dogs aged 11 and older comprised 5% of our dataset. We observed greater variation in cognitive
350 performance in older dogs, particularly among the oldest dogs in the study. For many tasks, the performance of the
351 oldest aged dogs in our study ranged greatly, often spanning the full spectrum of the dependent variable's range. The
352 relatively small number of very old dogs means that assessing cognitive performance in this group is more
353 susceptible to the influence of a small number of individuals. Future studies further establishing how cognition
354 changes and varies among this demographic would be valuable. We suspect that the limited number of very old dogs
355 may result from a selection bias in which owners of older, potentially highly impaired dogs, may have been less
356 likely to pursue participation in these activities. Thus, active recruitment of the oldest dogs will be an important
357 priority for future research. While collecting self-reported data from dog owners enabled the relatively large sample

358 size of this study, we had variation in the reporting of information such as training history, which decreased power
359 to detect effects of aging and possible associations with mean breed lifespan within this group. It will be important
360 to generate larger datasets in the future that can include other potentially relevant covariates. We also collected data
361 from dog owners at a single time point which limited the degree to which we could evaluate individual variation in
362 cognitive performance throughout aging. Lastly, the cognitive assessment we used included diverse tasks, but the
363 particular cognitive processes measured by each specific task were not unambiguous.

364 Due to extraordinary intraspecific phenotypic diversity, dogs present a unique model for investigating how
365 age-related traits vary with cognition across the lifespan. Our findings suggest that age-related changes in executive
366 function in domestic dogs follow patterns similar to those in humans and provide insight regarding the relationships
367 (or lack thereof) between life history and cognitive trajectories in a species characterized by extensive intraspecific
368 diversity. An important priority for future work will be to determine whether dogs and humans share similar aging
369 trajectories in other cognitive domains such as long-term memory, cognitive processing speed, and episodic-like
370 memory. Using consistent and readily deployable cognitive assessments, such as the ones presented here, future
371 studies could evaluate longitudinal changes in cognitive performance of the same cohort of dogs across various
372 timepoints to gain a finer grained understanding of dog cognitive aging.

373

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379

380 **Author Contributions** MMW, ELM, BH, and NSM conceived of the project. MMW, ELM, and NSM analyzed the
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387

388 **Compliance with Ethical Standards**

389 **Conflict of Interest** BH is the founder of *Dognition.com* and is a member of the *Dognition.com* Scientific Advisory
390 Board along with JC, JK, and ÁM.

391

392 **Data Accessibility** The dataset analyzed during the current study is not publicly available due to third party
393 restrictions but is available from the corresponding author on reasonable request and permission of Canines Inc.

394 Supplementary Materials associated with this article are available online. Code used to complete the described

395 analyses is available at <https://github.com/mwatowich/Dog-cognition-across-aging>.

396

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