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Dog Pups' Attractiveness to Humans Peaks at Weaning Age

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ABSTRACT The domestic dog (Canis lupus familiaris) is characterized by greatly reduced parenting investment compared with the wild type wolf (C. I. lupus) from which it is descended. Unlike wolf pups, which are reared by both parents into their second year of life, dog pups are abandoned by their mother at weaning around eight weeks of age. This relatively small parental involvement may contribute to the high pup mortality observed in dogs not living as pets. We hypothesized that people would find dog pups most attractive around weaning age when conspecific parental care is significantly reduced and pup mortality rate is high. Younger and older pups would benefit less from human intervention because in the former case the mother is providing care, and in the latter their survival is already compromised. To test this hypothesis, 51 participants rated the attractiveness of 39 black and white headshot photographs presented on a computer screen of dog pups from three breeds (Jack Russell Terrier, Cane Corso, and White Shepherd), from birth to 7 months old. In line with our hypothesis, attractiveness of Cane Corsos peaked at 6.3 weeks of age; Jack Russell Terriers' attractiveness peaked at 7.7 weeks; and White Shepherds were most attractive at 8.3 weeks. There were also differences in attractiveness between the breeds, with Cane Corsos rated less attractive than the other two breeds. If this attractiveness motivates humans to care for the dog pups and thereby improves pup survival, this could confer significant advantages to dogs, and may contribute to our understanding of the process of domestication.

Keywords: attractiveness, dog pups, human-animal interaction, Kindchenschema.



Dogs were the first animal species domesticated, originating from populations of wolves that adapted to human proximity (Clutton-Brock, 1999). The mechanism by which dogs evolved,

however, is still debated. Some authors have argued that the dog arose as a response to a new symbiotic relationship that formed with the

growing settled human populations at the end of the last ice age, thereby providing an ecological niche with new evolutionary selective pressures (Coppinger & Coppinger, 2001); others have proposed that the physical and behavioral changes that led to the formation of dogs were the outcome of human intervention and consequent artificial selection (Darwin, 1871; Derr, 2013; Morey, 1994; 2012). At different points in the history of the dog, natural selection in response to changing environments and human-determined artificial selection both likely played roles (Larson et al., 2011).

Regardless of the mechanism, the domestication of the dog resulted in diverse physiological and behavioral changes, which have been characterized as a paedomorphism of wolves (Morey, 1994; 2012). Compared to a wolf of the same weight, a domestic dog has a head that is 20% smaller, as well as a smaller brain and teeth (Coppinger and Coppinger, 2001). Other changes that occurred during domestication are defined by Coppinger and Coppinger (2001) as saltations: traits that appeared within a short time frame due to selection, such as floppy ears and variety of coat colorings.

Some of the most striking behavioral differences between the dog and wolf are in reproductive behavior (summarized in Lord, Feinstein, Smith, & Coppinger, 2012). Wolves show seasonality and reproduce once a year during a fall/winter breeding season. In contrast, male dogs are continuously sexually active; bitches only show a slight tendency toward seasonality (Pal, 2003; Boitani & Ciucci, 1995), and can return to estrus soon after giving birth (Lord et al., 2012). Wolves form long-term pair bonds, whereas dogs are typically promiscuous (Boitani & Ciucci, 1995; Pal, 2005). Wolf parents cooperate in rearing their young: among dogs, typically only mothers invest in raising young (Boitani & Ciucci, 1995; Kleiman & Malcolm, 1981; though see Pal, 2005, for some evidence of paternal investment, and Paul, Majumder, & Bhadra, 2014 for evidence of grand-maternal care).

Furthermore, wolf offspring stay with their parents for up to two years, receiving support from other family members when first weaned, and usually remain with their parents to assist in provisioning the young of at least one subsequent litter. Dog pups, conversely, are abandoned by their mother at weaning (between 6–11 weeks; Malm & Jensen, 1996; 1997; Pal, 2005; 2008; Paul, Majumder, & Bhadra, 2014; Wilsson, 1984). At first, dams start to reduce time spent nursing around the fourth and fifth week of a pup's life, both in captivity (Malm & Jensen, 1996; 1997; Wilsson, 1984) and in free-living (Pal, 2008) individuals. Weaning is usually complete around week eight in captive dogs (Malm & Jensen, 1996; 1997; Wilsson, 1984), and slightly later in free-living animals (10–11 weeks in India, Pal, 2005; 2008).

Dogs' low parental investment likely contributes to the high rate of pup mortality in pups not in the care of humans. The lowest estimate of the rate of pup mortality for free-roaming dogs is near 45%, estimated in Baltimore in 1971—though this was noted as an underestimate due to the difficulty of locating very young dogs (Beck, 1973). All other estimates are over 80% mortality in the first year of life. For example, Pal (2001) reported 82% first-year mortality in free-ranging urban dogs in Katwa, West Bengal, India. Boitani & Ciucci (1995) reported 95% first-year mortality in central Italy over a three-year period. Similarly, Macdonald and Carr (1995) reported 84% mortality in just the first five months of life in central Italy. Daniels and Bekoff (1989) estimated the survival rates to four months for the dogs in Cuidad Juarez, Mexico and Navajo reservation, Arizona, USA to be 66%. In New Providence, Bahamas, Fielding and Plumridge (2005) reported 45% mortality to the first birthday of owned (though largely free-roaming) dogs.

The limited post-weaning parental investment of dogs likely contributes to low pup survival rates in free-ranging populations. Therefore, having humans adopt and care for pups around weaning, could confer significant competitive advantages in survival. Human adoption *prior* to weaning may not have strong advantages as the pups already have conspecific parental care in place. Later human adoption would likely have little competitive advantage as most pups die within the first months to year of life (e.g., Macdonald & Carr, 1995). Thus, dog pups are most susceptible to death and most likely to gain significant benefits from human adoption at weaning. We hypothesize that dog pup morphology is most attractive to humans at or near the typical time of weaning.

Prior researchers have noted that adult dogs generally have paedomorphic features compared with wolves (Morey, 1994; 2012), and have suggested this enhances humans' attraction to the morphology of the dog. Lorenz (1943) was one of the first to propose that humans tend to be attracted to individuals with more juvenile physical features. An enlarged head with protruding forehead, large low-set eyes, a round face with bulging cheeks, and a small mouth and nose are the main features of the "Kindchenschema" (infant or baby schema), which is postulated to motivate a caregiving response in humans, regardless of the species carrying these features (Lorenz, 1943). Supporting Lorenz's hypothesis, Archer and Monton (2011) demonstrated that pictures of human infants, teddy bears, dogs, and cats with more infantile features were rated as more attractive than those that looked less infantile. Kindchenschema effects have even been noted in the evolution of fictional characters toward a shape more like that of juvenile humans in Mickey Mouse (Gould & Lewontin, 1979), and teddy bears that evolved from having long snouts into shorter snouted and larger round headed creatures (Hinde & Barden, 1985; Morris, Reddy, & Bunting, 1995).

These prior studies, however, have assumed that infantile features are attractive, without considering whether there might be an optimal age of attractiveness below which an infant animal might appear less attractive. To test the hypothesis that humans may find dogs most attractive at weaning (compared with younger or older dogs), pictures of the faces of three breeds of dog at a range of ages chosen to cover the typical age of weaning were presented to adult human participants who rated them for attractiveness. The breeds were chosen for the availability of series of photographs showing individuals in similar poses at a dense set of ages, and for their diverse, but not explicitly paedomorphic, appearance in the adult. The three dog breeds were Jack Russell Terrier, a small breed, originally used in fox hunting, of a typically pale coloration with short hair; Cane Corso, a large, darker-colored, originally guarding breed of dog; and White Shepherd, a large white, longer-haired, originally sheep-herding dog.

Methods

Participants

The study was approved by the Institutional Review Board of the University of Florida (Approval # u-774-2013). Fifty-one students (28 men, 23 women) were recruited through the Department of Psychology Research participation pool. Their ages ranged between 18 and 35 years (M=19.24, SD=2.78). Participation was voluntary, a signed informed written consent was obtained from all participants, and participation credit was awarded for attending the study, regardless of whether it was completed. All participants completed the study in its entirety.



Figure 1. Sample images presented to participants. The center column shows, for each breed, the most attractive image. In the case of the Cane Corsos, this is the six-week-old pup; for the Jack Russells, the seven-week-old pup; and for the White Shepherds, the eight-week-old pup. The left column shows the least attractive image younger than the most attractive (in all cases, the zero-week-old pups), and the least attractive image older than the most attractive is in the right column (in all cases the seven-month-old dogs). Top row: Cane Corso; middle row: Jack Russell Terrier; and bottom row: White Shepherd.

Stimuli

The stimuli were 39 black and white photographs of dogs from three breeds: Cane Corso (13 photographs, at the ages of 0, 2, 3, 4, 5, 6, 7, 8 weeks, and 3, 4, 5, 6, 7 months), Jack Russell Terrier (12 photographs, at the ages of 0, 1, 2, 3, 4, 5, 7, 8 weeks and 3, 6, 7, 8 months), and White Shepherd (14 photographs, at the ages of 0, 1, 2, 3, 4, 5, 6, 7, 8 weeks and 3, 4, 5, 6, 7 months). All photographs showed the dogs as frontal headshots with closed snouts, and were square (9.5 cm x 9.5 cm) with neutral backgrounds, and equalized in brightness. The images were presented singly on a computer screen and each participant saw the images in one of four random orders. Figure 1 includes a sample of the photographs presented to participants. Each participant was asked to answer the question "How attractive is this dog?" for each photograph by moving a slider to any spot between end positions marked "not at all attractive" and "very attractive." The software subsequently

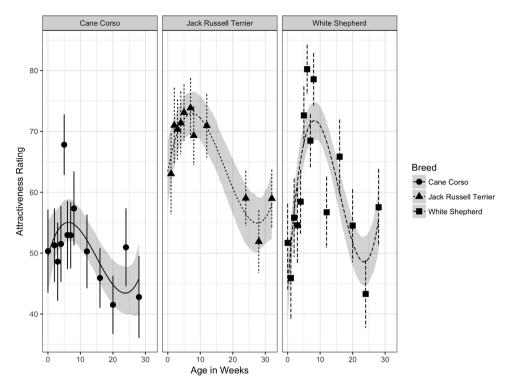


Figure 2. Attractiveness ratings as a function of age from 0 to 32 weeks for three breeds of dogs. Points show the mean attractiveness rating at each age. Error bars show the 95% confidence interval. Lines show the population level model estimates (random effects not included) and the shaded region shows the bootstrapped 95% confidence interval estimates from the model.

reported the spot chosen by the participant as a value between 0 and 100. A total of 1,938 ratings was scored.

Procedure

Participants signed up online through the Department of Psychology Research Participation Credit Manager. The study was located in a room at the Psychology building of the University of Florida. On arrival, the participant reported his or her name, age, and gender, and received an explanation of the study (but not its hypothesis) and written consent was obtained. Participants were led singly to a computer and asked to read the instructions on the screen. The experimenter sat at the side of the room while the participant completed the study.

Statistical Analyses

Linear mixed effects models were used to model rated attractiveness as a function of pup age and breed using the Imer4 package in R (Bates, Maechler, Bolker, & Walker, 2013). The ImerTest package was used to calculate p-values for the parameter estimates using a Satterthwaite's correction for degrees of freedom (Kuznetsova, Brockhoff, & Christensen, 2013), and the car package (Fox & Weisberg, 2011) was used to conduct Wald Chi-Square tests to test the effects of variables with more than two groups. Bootstrapped estimates were

Table 1. Wald chi-square goodness of fit parameters of the cubic model.

	df	χ^2
Age ³	1	91.80***
Age ²	1	121.65***
Age	1	122.47***
Breed	2	234.43***
Age ³ : Breed	2	27.34***
Age ² : Breed	2	34.15***
Age: Breed	2	43.48***

^{****}p < 0.0001, and superscripts are indicators of power (i.e., "2" = squared, "3" = cubed).

calculated using the boot package (Canty & Ripley, 2014). Models were inspected for violations of the assumptions of normality with q-q plots and homoscedasticity with residual plots.

Results

Figure 2 shows the overall rating of attractiveness for each breed of dog as a function of age in weeks. Attractiveness is low at birth, but then increases to a maximum before 10 weeks of age and declines again before leveling off. Finally, there is a possible small increase in attractiveness at the oldest ages tested. A cubic mixed effects model was fit to model this observed trend in the data. First, a cubic model that included all interactions with breed, age, and participant gender was fit with random intercepts for each subject. A comparison between this model and a model including random slopes across ages, indicated that a random intercepts and slopes model was a better fit ($\chi^2 = 137.24$, df = 2, p < 0.001). We then attempted to reduce the fixed effects through model selection. Participant gender had no significant interaction with breed, age, or main effect on participant ratings (p > 0.05), and was therefore removed from the model. All remaining interaction terms were highly significant and could not be reduced further, indicating that the cubic fit was the best-fitting model. Table 1 shows the Wald χ^2 values for each model parameter of the final model.

Figure 2 includes the best-fit and 95% Confidence Interval (CI) for the model considering fixed-effects only (grey shade). Overall, the shape of the curve for attractiveness varied as a function of breed, as indicated by the significant breed by age interaction as shown in Table 1. There was also a main effect of breed on attractiveness ratings ($\chi^2=234.43$, df=2, p<0.0001), where the Cane Corso was rated as the least attractive (see Figure 2).

To test the main hypothesis that dogs are likely to be most attractive at the age of weaning, we calculated the 95% CI intervals for the maximum value of attractiveness as predicted by the model for each breed. Bootstrapped confidence intervals were calculated from the maximum value of attractiveness from 400 simulations for each breed. Cane Corsos showed a maximum attractiveness at 6.3 weeks of age (CI: 4.1–8.2 weeks). Jack Russell Terriers showed a similar age of maximum attractiveness: 7.7 weeks (CI: 5.7–9.1 weeks), and White Shepherds were most attractive at 8.3 weeks (CI: 7.7–8.9 weeks).

Discussion

These results support our hypothesis that the attractiveness of puppies' faces from three distinct dog breeds does not decline monotonically with increasing age, but rather peaks around the time of weaning (6 to 8 weeks post partum) and is lower in both older and younger dogs.

The benefits to dogs of being cared for by humans would appear self-evident, especially once dams wean and abandon their young, but it should also be noted that Pal (2005), studying reproduction and infant mortality in free-living dogs in an Indian town, noted that the single largest cause of death in dogs in the first three months of life was their being removed as pets by children. This human intervention was responsible for 27% of all recorded deaths of pups in that age range. Nonetheless, it seems reasonable to suppose that human care of weaned pups aids the dogs' survival overall.

One prior study includes evidence that the Kindchenschema effect is not a monotonically increasing function of decreasing age of dog pup stimuli. Sanefuji, Ohgami, and Hashiya (2007) asked adult human participants and children around five years of age to sort seven photos each of human babies, a chimpanzee, rabbits, dogs, and cats of different ages according to their cuteness. Trends in cuteness as a function of age were not apparent for most of the species presented; however, dog pup cuteness clearly peaked at an intermediate age. The dog photographs were of the Shiba Inu breed at the ages of 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 months. Sanefuji et al. (2007) found that dog pup cuteness peaked at 1 month for adult raters, and 1.5 months for child raters. Both younger and older dogs were rated as less cute. The data analysis provided by Sanefuji et al. (2007) does not permit estimation of whether their age of peak attractiveness differs significantly from that obtained here, but, given the age difference in the photos they used, their data appear approximately consistent with our findings.

In addition to a significant effect of age on attractiveness for each dog breed, we also found that the breeds differed in their attractiveness. The Cane Corso was rated as less attractive than the other two breeds. This could be due to the darker color of the Cane Corso than the Jack Russell Terrier or White Shepherd. Some studies report that darker dogs are adopted from shelters slower than paler colored dogs: (Lepper, Kass, & Hart, 2002; Posage, Bartlett, & Thomas, 1998; Wells & Hepper, 1992); though this effect is not found at all shelters (Protopopova, Gilmour, Weiss, Shen, & Wynne, 2012). The Cane Corso might also be considered a more aggressive-looking breed than the other two tested here. Fighting breeds were the slowest to be adopted in Protopopova et al. (2012). The lower attractiveness of the Cane Corso may also be due to its larger size. Smaller dogs have been found in previous studies to be rated more attractive and adopted more rapidly from shelters (Protopopova et al., 2012). Smaller stature can also accentuate the Kindchenschema because the eyes of smaller dogs may appear bigger in respect to the face (Glocker et al., 2009).

Several studies have investigated the structural dimensions that underlie human perception of the attractiveness of human and nonhuman young. Glocker et al. (2009) observed that manipulated images of human infants high in Kindchenschema were perceived as cuter and more likely to elicit care-giving in manipulated photo-realistic stimuli. Little (2012) manipulated photographs of human and cat faces to look more or less infantile. He reported that human infant and cat faces were rated more attractive than adult human faces, and faces manipulated to look more infantile were rated more attractive in both species.

Baby-like facial traits in older children and adults can also be perceived as more likeable and attractive (Luo, Li, & Lee, 2011). Hecht & Horowitz (2015) systemically manipulated 14 attributes in photographs of dogs' faces and found that human observers preferred some

features associated with Kindchenschema, as well as human-like qualities such as colored irises and an upturned (smile-like) turn to the mouth.

One limitation of the present study is that only three breeds were deployed. Hundreds of dog breeds are recognized by breed clubs around the world and they display great phenotypic variation. This variability also extends to their appearance at different stages of development, making it possible that age at peak attractiveness to humans may vary considerably. Further, we did not ask about participants' familiarity with the breeds chosen, which may have had potential effects on their ratings.

A second limitation of the present study is that participants were invited to rate still photographs of the dog pups. Ratings of video—or even live viewing of the pups—could have produced different results due to the attractiveness of the animal's patterns of movement. Although most discussions of the Kindchenschema hypothesis have focused on the cuteness of static animal faces, Lorenz did mention "clumsy movements" as part of the Gestalt of Kindchenschema (Lorenz, 1943). In life, if there is an adaptive function to the process of interspecies attractiveness of juvenile individuals, it must be revealed in ecologically realistic viewing of live individuals. One study that considered attractiveness of a live pup found that attractiveness measured as the approach of strangers to a person holding a pup, decreased with increasing pup age. However, the youngest pups tested in that study were already 73 days (10.5 weeks) old (Fridlund & Macdonald, 1998).

A third limitation to this study is that the participants were young-adult university students. Different populations of human observers might show different patterns of attractedness to dog pups of different ages.

The present results indicate that these three breeds are rated most attractive around weaning. Any possible adaptive explanation of this cross-species attraction must remain highly speculative, but the possibility that dogs and humans may have co-evolved so that dogs are most attractive to people just at the point where human intervention would have the most positive impact on pup survival may contribute to developing an understanding of the mechanisms of domestication. Future research could extend these findings to other breeds, to the perception of live pups, and also investigate the structural components, such as relative size of different facial components, underlying the preferences found here.

In conclusion, in three breeds of dogs, pups were found to be most attractive to human raters around weaning age, which is a time of high mortality for dog pups. This attraction of humans to dog pups at that phase of life may have given early dogs, and may continue to give today's free-living dogs, a competitive advantage by being adopted and cared for by humans as conspecific care decreases.

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Conflict of interest

The authors affirm no conflict of interest arises in this study.

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