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Research

Domestic dog skull diversity across breeds, breed groupings, and genetic clusters

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ABSTRACT

Domestic dogs have become a model organism for studying the extent and consequences of morphological diversity, especially in the skull. It has been demonstrated that Cephalic Index (CI, skull width/skull length) correlates with central concentration of ganglion cells in the retina and with ventral rotation of the cerebral hemispheres. These changes may be reflected in the behavior of breeds with different skulls shapes. This study explored skull variation in the breed groups ($n = 7$) described by the Australian National Kennel Club to determine if CI differed significantly among the breed groups; groups were expected to differ not least in behavior. The CI of 12 representative dogs (females, $n = 6$; males, $n = 6$) of the most popular breeds ($n = 80$; total $n = 960$ dogs) were measured. Multivariate analysis of variance was performed to determine CI variance among the breed groups and between previously reported clusters of breeds with similar DNA, which identifies common ancestry. Although CI differed significantly among some breed groups, neither the breed groupings nor the DNA clusters satisfactorily explained all the variance in CI. The results show that breed groupings and genetic clusters only partially explain CI differences. They also suggest that CI is on a continuum and that the definition of three categories of canine skull as dolichocephalic, mesocephalic, and brachycephalic may be overly arbitrary.

Introduction

Since domestication, dogs have played many important roles in human life. These traditionally included hunting, guarding, and herding, and the dogs are now a valuable source of companionship in many family homes. Historically, the number of dog breeds grew rapidly from the mid-19th century, and there are now more than 400 recognized breeds. Research on dog skull morphology has been conducted for almost as long. In particular, Studer (1901) used skull morphology to determine five putative original clusters within modern breeds. Purebred dogs are grouped into categories that reflect not only their common ancestry and geographical origins but also their functional and behavioral attributes. Dog breeds vary not only in size but also in their conformation, coat attributes, and brain case positioning (Drake and Klingenberg, 2010). Common categories used by kennel clubs (KCs) and councils (the umbrella organizations that govern the rules of dog showing and pedigree dog breeding) include herding, retrieving, hunting, guarding, toy, sporting, and miscellaneous. Of course, the dogs have also been used for haulage and indeed for their meat. Different behaviors have been selected for or against during domestication, and these are now echoed in the written breed standards against which show dogs are judged. Yet because there are only limited opportunities to judge temperament and behavior in the show ring, breed selection has tended to focus on appearance rather than behavior. Some have questioned the logic of this practice because modern purebred dogs are mainly kept as companions rather than for a breed-specific purpose (McGreevy and Bennett, 2010).

Genetic similarities and differences are another approach to breed classification that avoids problems associated with subjective value judgments. VonHoldt et al. (2011) classified breeds based on DNA linkages to suggest 10 genetic clusters, such as toys, spaniels, scent hounds, working dogs, mastiff-like dogs, small terriers, retrievers, herders, sighthounds, and ancient/spitz breeds. Interestingly, variability in skull shapes has recently been described as

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having multiple genetic loci, particularly in relation to the degree of brachycephaly (Schoenebeck et al., 2012).

Morphological diversity has been described in numerous species, but dogs (*Canis lupus familiaris*) exhibit the greatest variation, especially when compared with their ancestral relative, the wolf (*Canis lupus*) (Drake, 2011). Most breeds of dogs have phylogenetically novel skull shapes when compared with adult wolves (Drake and Klingenberg, 2010). Breed-to-breed variability also applies to the canine skull, so it is unsurprising that breed standards often devote considerable detail to skull attributes. Of the various phenotypic attributes, it appears that skull shape has been subjected to the most scientific scrutiny. Cephalic Index (CI) is a simple method of characterizing skull morphology. In humans, the terms dolichocephalic, mesocephalic, and brachycephalic are applied to skulls with different shapes based on the CI. The same terms are used in canine anatomy, but the thresholds between one category and another have not been defined.

Skull shape is important because it may have a bearing on brain function and behavior, a question of enduring interest to evolutionary biologists and veterinary scientists (McGreevy et al., 2004). Reduction in skull length in carnivores correlates with a reduction in olfactory lobe size, hypothetically owing to restriction in the development of frontal brain regions (Gittleman, 1991). This also appears to be associated with a truncated behavioral repertoire (Goodwin et al., 1997). There is recent evidence that the behavior of dogs co-varies with skull shape (McGreevy et al., 2013).

Variation in skull length is also associated with differences in retinal ganglion cell distribution (McGreevy et al., 2004), a potential explanation for an increased ability to focus in the central field of view rather than in the periphery and hence to respond to human pointing gestures (Gácsi et al., 2009). More recently, by examining magnetic resonance images (MRIs) of the brains of a range of dog breeds, Roberts et al. (2010) showed that the relative reduction of skull length compared with width (measured by a higher CI) was significantly correlated with a progressive pitching of the brain, as well as with a downward shift in the position of the olfactory lobe. This finding was confirmed by Hussein et al. (2012).

Heterochrony, a process that requires only simple genetic modifications to develop diversity, relies on changes in the timing or rate of ontogenetic pathways (Gould, 1977). Although previous research suggested that dogs evolved via heterochrony and are pedomorphic wolves (Coppinger and Coppinger, 1982, 2001; Frank and Frank, 1982), a recent study has challenged the role of heterochrony and concluded that dogs are not pedomorphic wolves. It used geometric morphometric analysis to investigate heterochronic patterns of the adult dogs ($n = 677$) representing 106 different breeds, and compared them with an ontogenetic series of 401 wolves (Drake, 2011). This revealed that none of the modern breeds of dogs had a cranial shape that resembled the cranial shapes of wolves. The study confirmed the earlier finding of ventral tilting of the cerebral hemispheres in association with brachycephaly (Roberts et al., 2010). Moreover, it reported tilting in the opposite direction in dolichocephalic and "down-face" breeds, such as the bull terrier. An additional examination of juvenile wolf skulls demonstrated that the position of the face and the neurocranium remain in the same plane throughout maturation (Drake, 2011). In summary, dogs show a small amount of genetic variation but an enormous range of phylogenetically novel skull shapes.

In this study, we screened a wide array of common breeds to assemble the largest report of CIs in dogs. This allowed us to establish whether interbreed CI variance was related to Australian National Kennel Club (ANKC) breed groupings, to known genetic clusters (VonHoldt et al., 2011) and to groupings used by the Federation Cynologique Internationale (FCI).

We also hypothesized that some variance in CI may reflect difficulty in measuring skull difference among smaller dogs, so we explored relationships between a breed's CI variance and some indicators of the average size of dogs within each breed. Another possible source of variability may be genetic diversity, so we estimated the size of the Australian population for each of the breeds in question by examining the number of puppies registered within the breed over the preceding 5-year period. A third possibility is that CI variance reflects a lack of detail in the breed standard about the preferred conformation of the skull. As a proxy for this detail, we examined the role, if any, of the word count for the description of desirable features of the "head and skull" for each breed as specified in the ANKC breed standards. Finally, with a large audit of this nature, we expected to be able to elucidate how the three categories of skull (dolichocephalic, mesocephalic, and brachycephalic) can be distinguished from one another.

Methods

Cephalic Index

The method was designed to ensure that the representative dogs of each breed were measured for skull attributes. We sampled six females and six males from each breed. To be included, dogs had to be aged 2 years or older and of show quality or from show-quality lines. Littermates of dogs that had already been measured were avoided to ensure that the effects of a certain mating were not amplified in the study.

To be included, breeds had to:

1. Be recognized by the ANKC
2. Be owned by the breeders registered with DogsNSW, and
3. Have had more than 30 puppies registered nationally with the ANKC in 2009.

Dogs were held by an assistant so that the nasal planum was horizontal and were then photographed using a dorsoventral view of the top of the head, which allowed the length and width of the skull to be measured. A standardized cloth strap with a rectangular benchmark (2.5 cm × 4.9 cm) was placed at the centre of the zygomatic arches. A finger placed on the occipital crest was placed and the photo was taken (Figure 1). The breed, dog's name, and age were all recorded.

Figure 1. A photograph of a Saluki, a dolichocephalic breed. For the present study, each photograph was taken with the camera held horizontally, which allowed measurements to be obtained for each dog's skull length and width. The length was measured from the fingertip to the tip of the nose, and the width was measured from each zygomatic arch, which was displayed by the tape placed around the widest part of the dog's head.