

Review

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Review

What Should Dogs Look Like? Welfare Consequences of Canine Morphology

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Abstract

The domestic dog has been intensively selectively bred since the Victorian era for morphological traits. Questions about the implications on canine welfare of some of those traits have been asked since that time. More recently, legislation has been proposed and enacted in several countries to guide selection for specific morphologies. We describe common canine phenotypes with associated disorders and the biological mechanisms driving those disorders. We additionally describe opportunities for further study identifying which ranges of morphologies support robust canine health while still preserving the uniqueness of different breeds. Focusing on morphologies with a range of expression, rather than focusing on harmful characteristics prevalent in particular breeds, is a new perspective on canine welfare which we expect to support evidence-based efforts to set future breeding goals, and to increase awareness of these issues by the people who purchase [and love] dogs.

Keywords: dogs; animal welfare; canine welfare; canine health; animal breeding

1. Introduction

The domestic dog is the most morphologically diverse mammalian species [1], in part because of the species' unique evolutionary history [2]. Dogs arose 11,000 to 40,000 years ago [3–5] from a population of gray wolves that is now extinct [3,6–8]. Like free-living village dogs today, early dogs were human commensals subject to natural selection [9]. Around the Early Bronze period, several cultures began to manage dog populations to form loosely defined types [10–13]. While it is debated when the first dog breeds were formed [14], the oldest dog breeds in existence today are based on landraces which developed around 500 years ago for functions such as hunting or pulling sleds [15,16], although some have argued for potential earlier emergence [17].

By contrast, most extant dog breeds have much more recent origins [18]. British dog enthusiasts of the late Victorian period were interested in improving the appearances of dogs, which led them to establish breed standards and narrow gene pools [19–21]. In many dog breeds, this facilitated selection for novel morphologies that did not exist prior to this period, such as severely shortened snouts [22]. While many Victorians admired dogs with these traits, some called them “monstrosities” [20]. More recently, in several European countries legislative attempts have addressed concerns about extreme morphologies in light of growing scientific evidence that they are associated with compromised welfare [21,23–26] and the first American municipality has banned the breeding of specified morphologies [27]. Many of the concerning traits may cause pain, which has secondary effects on behavior [28].



Figure 1. George Du Maurier, “Dog Fashions for 1889.” *Punch*, 25 Jan. 1889.

This review provides a broad overview of common canine phenotypes with associated disorders. We detail biological mechanisms where they are understood, as well as resulting welfare implications. We argue that clearly defined guidelines are a necessary part of any attempt to modify dog breeding to be more favorable to canine welfare. We hope this review will serve as a base for future work developing those guidelines, which may be of use when extreme morphology becomes a welfare issue, to support evidence-based efforts to set new breeding goals, and to increase awareness of these issues by the people who purchase (and love) dogs.

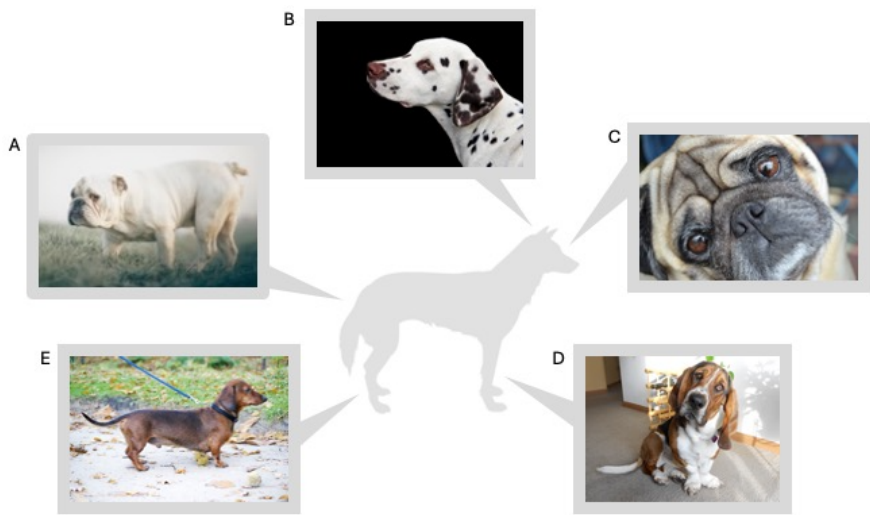


Figure 2. Extreme morphologies selected for in dog breeds. A. “Screw tail,” associated with congenital vertebral malformations, which in turn are associated with kyphosis and intervertebral disc herniation. B. Extreme white coat color, associated with deafness; spots, associated with urinary tract stones. C. Brachycephaly, associated with brachycephalic obstructive airway syndrome, ocular disorders, skin fold infections, ear infections, and GI disorders. D. “Wrap-around front” legs, associated with angular limb deformity. E. Chondrodystrophy, associated with intervertebral disc herniation.

2. Size

Dogs have a wide range of sizes, ranging from the Chihuahua (which can stand under 15 cm tall and weigh just 1.5 kg) to the Irish Wolfhound (up to about 94 cm tall) and Mastiff [up to about 105 kg]. An IGF-1 polymorphism is the largest single contributor to the size variation in selectively-bred dogs [29,30], but variations in other genes also play a role in determining canine size [31–34]. Comparisons between breeds of dramatically different sizes indicate that IGF-1 genetic differences influence circulating hormone levels, which decline throughout life from an early postnatal high, suggesting that IGF-1 variation influences body size by influencing growth rate [35]. Canine allometric scaling differs from scaling of similarly sized mammals of other species, and this difference may be associated with pathologies; for example, the brain, liver, lungs, and kidneys are larger in 2 kg dogs than other mammals of similar size, and smaller in 70 kg dogs; gestation length is fixed in dogs across all sizes, despite being closely correlated to size in other mammalian species [36]. Variation in body size has far-ranging impacts on other traits as well, which we outline in the following sections.

2.1. Lifespan

Small dogs are well known to live longer than larger dogs [37], with a predicted lifespan difference of 4.5 years between dogs of the smallest and largest breeds [38]. This difference is relatively smoothly graded; a 1 kg body mass increase between breeds is associated with about 26 days' decrease in expected lifespan [38]. The expected lifespans of giant breed dogs are notably short; their age of senescence [i.e., the point of lowest risk of mortality, after which mortality risk begins to increase] can fall before they have reached their full adult growth [39]. Larger dogs have also been found to receive more veterinary care throughout their lives [40].

Larger dogs are more likely to die at every time point once maturity is reached, and the speed of increase of this mortality hazard is positively correlated to body size [37,39]. Postnatal growth rates are negatively correlated with lifespan in mammals [37,41] and large breed dogs grow faster and longer to reach their larger size [35,42] - early growth rates increase by an average of 0.22 kg/week per 10 kg of adult size [37]. This difference in growth rate is most likely primarily driven by differences in circulating levels of IGF-1. Differences in levels of this hormone are associated with longevity differences across species, from nematodes to mammals; in mammals, reduced IGF-1 signaling is associated with increased longevity [43].

While the correlation between size and lifespan has been well documented in dogs, existing analysis has focused on describing correlation across the complete size range. Does an inflection point exist in the relationship between size and lifespan? In other words, how big is too big? Answering this question may help guide future breeding programs.

2.2. Cancer

As dogs increase in size, so too increases their risk of cancer [37,38,43–46]. The correlation between weight increase and risk of mortality due to cancer is linear from toy to small and medium sized dogs; the line flattens for large and giant sized dogs, likely because cancer is typically a disease of old age, and larger breeds have such reduced lifespans that they do not live into the age range of high cancer risk [46,47].

Why are larger dogs at higher cancer risk? Within a species, species-specific protective mechanisms are likely to be ineffective for individuals of unusually large size. This predicts that larger dogs will have greater cancer risk, which [while allowing for some cancers specific to specific breeds] has been demonstrably true [37,48]. The size-cancer risk relationship is well illustrated by canine osteosarcoma. This disease primarily affects the long bones of the limbs in dogs [48,49]. The mortality related to this disease is high, with a one year survival rate of around 45% [50]. Risk of osteosarcoma in dogs is associated with size: dogs weighing over 60 kg have more than 36 times the

risk of developing osteosarcoma compared to dogs of 10-20 kg [51], though height may have a stronger influence on risk than weight alone [52].

It is likely that the increased growth rates in large and giant breed dogs, required to generate such long bones, is the strongest driver of osteosarcoma risk, rather than breed-specific mutations or environmental risk factors [48]. Indeed, genome wide association studies of canine osteosarcoma have found associations between the disease and genes associated with growth: IGF-1 [53], described previously; FGF9 [53], a gene associated with long bone development [54]; and CDKN2A/B [54,55], tumor suppressor genes which operate through interactions with the cell cycle [54–56]. Therefore, the most effective preventive approach for this disease may be to breed dogs of less extreme size [51], though the ideal size range for reduction of cancer risk is unknown.

2.3. Orthopedics

The welfare impacts of different orthopedic disorders vary. However, all of them predispose dogs to development of secondary osteoarthritis [57], a disease typically associated with old age which is very commonly diagnosed and can lead to pain and associated decrease in quality of life [58]. Increasing body weight is also associated with risk of osteoarthritis, though frame size has not been well separated from body condition in the literature [58,59].

While large dogs have been found to be at higher risk of orthopedic disease overall [44,46], small dogs are more susceptible to some specific orthopedic disorders, most commonly patellar luxation, with dogs under 10kg having 2.8 greater odds of diagnosis compared to dogs in the 10-19.9 kg range [60]. Canine hip dysplasia (CHD) is a common developmental disorder in which the hip joint is malformed, potentially causing lameness in young dogs, but more commonly resulting in osteoarthritis in older dogs [61]. This disease is more common [or more commonly clinically symptomatic] in medium sized dogs and larger, particularly large and giant sized dogs [62–64]. Another common developmental orthopedic disorder of large dogs is elbow dysplasia, an umbrella term for a suite of disorders which may, together, significantly contribute to the later development of osteoarthritis [65,66]. In one study, the risk of elbow dysplasia increased steadily from a baseline of dogs under 10 kg to 15.03 times the odds in dogs over 40 kg [66]. One of the most common orthopedic injuries in dogs is to the cranial cruciate ligament (CCL) [67]. While the etiology of CCL disease is complex, large dogs are diagnosed with it at younger ages [67–70] and greater frequencies overall [67,68]. The preponderance of studies about risk of orthopedic disease in dogs are breed-specific, and direct analyses of the connection between frame size and risk are needed for many disorders.

2.4. Heart Disease

Small dogs are more likely to be diagnosed with cardiac disease [46]: 75% of breeds averaging under 9 kg suffer cardiac disease as a major cause of death, versus only 25% of breeds averaging over 9 kg [71,72]. The type of cardiac diseases common in small dogs differ from large dogs as well; small dogs are more likely to be diagnosed with mitral valve disease (MVD) [71,72]. The cause is unknown, but hypotheses include a small chest crowding the heart, genes for small size which are known to affect heart development, or simply shared ancestry between many small breeds [71]. Large dogs, conversely, more commonly suffer from dilated cardiomyopathy (DCM), with increased risk reported in dogs over 30 lbs [73] and median weight of DCM cases around 37 kg [74]. Because of lack of coordinated studies of risk, there is no clear guidance around the range of frame size or bodyweight to most greatly reduce the risk of cardiac disease. Does risk spike above and below particular weight ranges? This question has not been addressed, and more studies of risk are called for [72], although medium sized dogs appear to be at lower risk.

2.5. Dental Disease

Risk of periodontal disease (PD - disease of the tissues surrounding the teeth and holding them in place) increases as adult body weight decreases [75]. Dog breeds averaging under 6.5 kg in adult body weight have been found to have up to five times the risk of PD compared to giant breeds, and the majority of dogs diagnosed with PD were from breeds of medium-small size or smaller [76]. Risk of retained deciduous teeth increases as adult size decreases, with a prevalence of 15% in extra small dogs compared to less than 1% in medium-large and larger dogs [77]. As for crowded teeth, smaller dogs may be at increased risk due to having teeth of a larger size relative to their skulls [78], and the consequences of disease in dogs of this size may be greater due to their relatively less alveolar bone [79].

2.6. Energy Regulation

Body mass affects energy regulation, with challenges at both extremes. Very small dogs have an elevated risk of hypoglycemia as a consequence of their low body mass index [80] and may need to allocate more of their metabolism to thermoregulation than larger dogs [81]. Conversely, larger dogs have more difficulty dissipating heat due to reduced surface area to volume ratio, and are at higher risk of heatstroke (dogs weighing over 50 kg have 3.42 times the risk compared to dogs under 10 kg) - an increasing problem in many parts of the world as global temperatures rise [82].

2.7. Labor Difficulties

Bitches at both extremes of size are at increased risk for dystocia (difficulty in labor) [83,84]. The risk for dystocia in small breed dogs is widely recognized, with an increased risk of 3.3 in toy breeds [83,84]. The mechanism for this is hypothesized to be the decreased litter size seen in smaller dogs, leading to larger individual puppy size and a mismatch between puppy size and the birth canal [36,83–85]. Dystocia in large breed dogs appears to have been less commonly studied; potentially, the larger litter size in large dogs [85] could lead to exhaustion of the uterine muscles during prolonged labor, which is a risk factor for dystocia [86,87]. Labor difficulties can also result from other extreme morphologies; see section 3.6.

2.8. Behavior

Behavioral differences have been described in smaller breeds, including increased risk of fearful and/or aggressive behavior [88–92] and decreased ability to follow human pointing gestures [93]. Meanwhile, trainability is positively associated with breed body size [88], and behavior scores can cluster by breed body size [94]. However, a study which included mixed-breed dogs and assessed individual rather than breed-average behavior scores suggested that individual (as opposed to breed) body size may not correlate with behavioral differences [34], suggesting breed differences may have more influence on behavior than size alone. Alternatively, small dogs may show reductions in neocortex, a component of the brain linked to trainability and behavioral flexibility, and enlargement in subcortical regions, which are linked to fear, aggression, and behavioral reactivity [95]. This recapitulates an allometric scaling pattern that has long been observed in a broadly cross-species context [96–98]. Alternately, behavior differences in small dogs could be due to differences in training and management, as owners of small dogs may be less likely to play with, train, and socialize them [91,92,99]. Size-based behavioral differences could be due to a variety of potential mechanisms, which could be distinguished through further research. These could include genetic influences, which are possibly breed-specific; neuroanatomical differences; visual perceptual differences; and/or differential training regimens by owners who are more likely to tolerate behavior issues in smaller dogs. Alternatively, simply living as a small dog in a big world may lower the threshold for threat perception and increase reliance on behaviors which mitigate perceived threat, such as reactive aggression.

3. Skull Shape

Skull shape varies across dog breeds from the very long and narrow (dolichocephalic) to the canid-average (mesocephalic) to the shortened muzzle and wide head (brachycephalic). Brachycephaly has shown dramatic increases in popularity over recent decades [100,101] despite many associated health disorders resulting in increased veterinary costs and decreased lifespans [40,100,101]. The attraction of the brachycephalic phenotype and cognitive dissonance in relationship to its welfare implications is an active area of study [101–104]. Future work may focus on the question of how to redirect public interest towards a healthier phenotype.

3.1. Brachycephalic Obstructive Airway Syndrome (BOAS)

The syndrome best associated with brachycephalic dogs is BOAS. Brachycephalic breeds have undergone artificial selection to reduce the bones of the muzzle; however, other structures of the head have not been reduced in concert. The resulting size mismatches in the brachycephalic head cause upper airway obstruction, the primary cause of the syndrome, which results in secondary pathologies due to chronically increased negative airway pressure. Sequelae as the disorder progresses include dyspnea (difficulty breathing), exercise and heat intolerance, increased airway sounds (snoring while awake), sleep apnea, gastrointestinal signs (such as reflux, regurgitation, or vomiting), collapse, and death [105–107].

Congenital soft tissue changes associated with the shortening of the muzzle begin at the nostrils, which may be narrowed to slits allowing little space for air passage. The soft palate is thickened, a change which may be primary [105–107] but may also be secondary due to chronic struggle to move air [108,109]. The brachycephalic tongue may be thickened, again either a primary or secondary change [110], which can block the upper airway. The trachea may be narrowed, further increasing airway resistance [105–107,110,111]. The nasal turbinates - a delicate bony structure in the sinus space, designed to support thermoregulation - may protrude into and impede the airway [112,113]. These various deformations may result in single to multiple points of mucosal-mucosal contact throughout the upper airway, i.e., blockages decreasing the space for air passage and causing increased negative airway pressure [112,113].

The disorder is often progressive due to this chronic resistance to airflow [114]. Secondary changes may include thickening of soft tissues such as the soft palate [108] and tongue [110], potentially followed by inflammation and degradation of the laryngeal tissue [105–107,111]. Laryngeal collapse may follow, i.e., temporary complete blockage of the airway [105–107]. The increased negative airway pressure may also affect the gastrointestinal tract, and BOAS is commonly associated with reflux, regurgitation, vomiting, and temporary herniation of parts of the stomach into the thoracic cavity [115,116]. Thermoregulation can also be markedly affected; an English Bulldog has been documented as hyperthermic while standing at rest in a temperature controlled room [117]. The majority of the canine airflow passes through the nostrils rather than the mouth, and thermoregulation through panting is most efficient when the air passes in through the nostrils and out through the mouth [118], meaning that decreases in upper airway airflow such as seen in brachycephalic dogs are particularly consequential for thermoregulation.

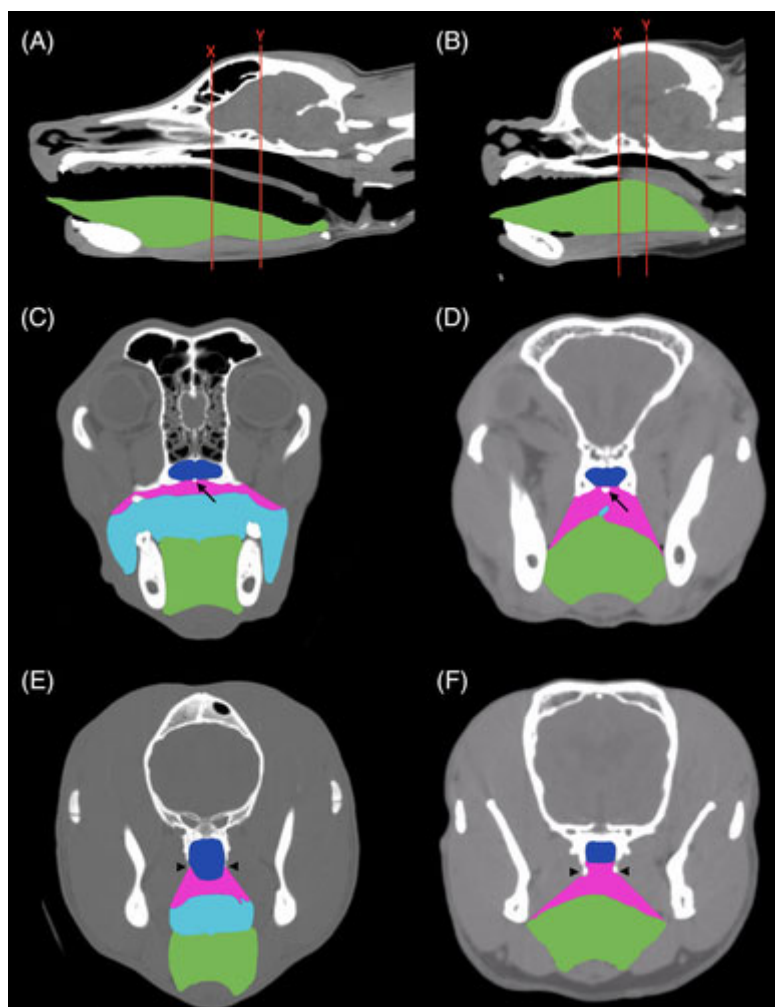


Figure 3. Computer tomography of mesocephalic skull (A,C,E) and brachycephalic skull (B,D,F). Tongue is highlighted with green. (Aqua represents the oropharynx, blue the nasopharynx, and pink the palatal tissues.) Note the difference in tongue thickness between the two skull types and its potential to block the airway (marked with red lines in A, B) [110].

BOAS is a complex set of changes and an individual dog may be diagnosed with one or more of them. Breed differences have been recognized, and appear to support the theory that reduced airway space further towards the nostrils (rostral) affects function more than reduced space further down the airway (caudal) [119].

3.2. Brain and Nervous System Abnormalities

The changes in skull shape associated with brachycephaly predispose many toy and brachycephalic breeds to disorders of cerebrospinal fluid [CSF] flow, Chiari-type malformation [CM], and syringomyelia (SM) [120–123]. CM is characterized by crowding of the brain and cervical spinal cord and is often associated with behavior indicating pain [121,122,124]. SM is closely associated with CM and, in many breeds, rarely seen in its absence [120]. It is defined as the presence of a cavitation (syrinx) in the spinal cord [121–123]. Dogs with a syrinx may be asymptomatic, but commonly present with signs including pain, reduced activity, phantom scratching, scoliosis, ataxia, and weakness [123,125,126]. In Chihuahuas, open cranial sutures (persistent fontanelles), commonly considered of no clinical consequence, are associated with SM [127]. SM has significant welfare consequences, as affected dogs commonly are treated with analgesics, and may be euthanized due to quality of life issues [123,126,128,129]. SM is often progressive due to compensation for blocked CSF flow [122,126,130,131]. Both CM and SM are strongly associated with a shortened, domed skull shape and

tighter angle between the nasal and frontal bone [124,132]; CM is almost fixed in some breeds with distinctively domed heads [Griffon Brussels 80% [121], Cavalier King Charles Spaniel (CKCS) 91-100% [120,131,133,134]]. SM is a more complex disorder but also at high prevalence in breeds with the risk head shape (e.g., CKCS 70-74% [133,135]). True prevalence of SM may be higher than reported as diagnosis requires MRI, an expensive and invasive test, and due to its progressive nature and potentially late onset [129,131,136]. While symptomatic SM is highly heritable [130,137], attempts to breed away from it have resulted in only minimal reduction of prevalence [138], perhaps due to the challenges of MRI-based screening, the disorder's causal association with a head shape that is considered desirable, and because of low variation of that head shape in the affected breeds [124,132,137,138].

Additionally, the brachycephalic phenotype may predispose to an increased risk of structural brain lesions associated with epilepsy [139].

3.3. Eye Disease

A short muzzle and compressed skull shape predispose brachycephalic dogs to eye disease, loss of the globe, and blindness, as reviewed in [140]. Corneal irritation and increased risk of ulceration arise from shallow orbits resulting in protrusion of the globe; nasal folds lead to caruncular trichiasis (hair rubbing on the surface of the eye); macroblepharon (abnormally large opening between the eyelids, resulting in decreased protection of the eye); decreased corneal innervation leading to decreased sensitivity; and lagophthalmos (incomplete blinking due to inability of the eyelid to cover the eye). The recurrent irritation and ulceration of the cornea increases risk for ulcerative keratitis and corneal pigmentation, resulting in potential loss of vision and of the globe itself. Shallow eye orbits also increase the risk of traumatic proptosis (the eye being displaced out of the orbit). Other increased risks include keratoconjunctivitis sicca, which also carries risk of blindness and loss of the eye, and prolapse of the nictitating gland of the third eyelid [140]. Exact risk differs by breed [141]. Increased risk for corneal ulcerative disease in brachycephalic compared to mesocephalic dogs has been calculated at 11.18 [142], but this may be an underrepresentation of the true prevalence of the disease in flat-faced dogs, as some forms of ulcerative disease may be challenging for primary care veterinarians to diagnose [141]. Constant irritation of the eye is painful, as are corneal ulcers, and ulcerative disease can contribute to euthanasia decisions [142].

Selective breeding to more moderate conformation can reduce these risks. Dogs with nasal folds may be at 5 times the risk of corneal ulcers compared to those without, and dogs with a craniofacial ratio < 0.5 are at 20 times the risk [143]. A 10% increase in the angle of the eyelid aperture triples the risk of ulcers, as does exposed eye white [144].

3.4. Ear Infections

Ear infections (otitis externa and otitis media) are a common health concern in brachycephalic breeds - the most common diagnosis in primary care for bulldogs [145] and third most common for pugs [146]. The brachycephalic head shape is associated with narrowing of the canal in the outer ear [147,148] which may result in drainage issues predisposing to infection [147]. Middle ear effusion is seen in brachycephalic dogs even when asymptomatic, again suggestive of drainage issues predisposing to infection [148,149].

3.5. Developmental Abnormalities of the Skull

Brachycephalic dogs are overrepresented in the population of dogs presenting with cleft lip or palate (CL/CP) [150–152]. While environmental influences and inbreeding likely contribute to this predisposition in addition to conformation [150,151], the developmental origins of CL/CP are suggestive of a link to brachycephalic conformation. Specifically, the hard and soft palate develop from a complex series of fusions of tissues from different developmental origins; this series is initiated by fusion of nasal and maxillary processes [153]. Moreover, CL/CP dogs frequently have other

craniomaxillofacial abnormalities visible on CT [154], indicating that these abnormalities may be associated with other developmental abnormalities that are more difficult to recognize. Notably, while brachycephalics are overrepresented among CL/CP diagnoses, dolichocephalics appear to rarely if ever suffer from this condition [151,152]. CL/CP is a welfare issue, as it may be commonly associated with neonatal euthanasia [154], surgery is the only definitive treatment [152], CL/CP surgery is complex and often requires multiple attempts for resolution [155], and surgery will not be curative in 15% of dogs [152].

3.6. Labor Difficulties

A mismatch between maternal pelvic opening and fetal head size is a common cause of labor difficulty (dystocia) [156–158]. Breeds with typically large heads, such as the English bulldog, Boston terrier, and French bulldog, are overrepresented in dystocia cases [83,156,157]. The true prevalence of dystocia among these breeds is difficult to assess, as most owners elect for Caesarean section. C-section rates in these breeds may be over 80% [156]; one report estimated 95% of English bulldog births were via C-section, of which 90% were elective [157]. Rates of dystocia in these three breeds are so high that some insurance companies will not insure against it [159].

4. Dwarfism

4.1. Chondrodysplasia

Canine “dwarfism” is caused by marked shortening of the limbs [160,161]. An *fgf4* retrogene in chromosome 18 results in chondrodysplasia, the most significant shortening of leg length [160,162], due to a disorder of cartilage cells in the growth plates [163]. While the limb shortening itself does not appear to be associated with welfare issues, in some breeds it is closely related to forelimb curvature, or angular limb deformity (ALD) [164], and the mutation has been linked to increased risk of rotation of the ulna (ulnar valgus) [160]. Chondrodysplasia increases the risk of complex ALD [165]. The retardation of ulnar growth due to the mutation can result in compensatory bowing of the radius to compensate, as well as a turned out carpus [valgus], both of which issues increase the risk of elbow joint disease at a much younger age than is expected in dogs with straight legs [166–170]. Shorter and more deformed the limbs are associated with greater joint space between the humerus and ulna and a greater risk of lameness [171,172].

Prevalence of this issue is challenging to assess, as it is considered normal for many breeds and therefore underreported [171]. For example, an AKC breed description notes that “Dachshunds aren't built for distance running, leaping, or strenuous swimming” [173]. This issue was recently introduced as one with significant welfare repercussions which is deserving of more study [164]. While the connection between chondrodysplasia and leg bowing appears not yet fully understood, bowed legs [or “crook'd legs”, or “wrap-around front”] and splayed carpi are explicitly called for in the conformation standards for the Skye terrier, dachshund, and Cardigan Welsh corgi, and in addenda to the Basset hound standard [174–176], and a guide to judging Bassets notes that “Bassets with straight front legs are called ‘wide’ in front. A wide front is incorrect” [177]. Therefore, it is possible that the *fgf4* insertion on chromosome 18 works in concert with another mutation to predispose to ALD, which has been selected for in some breeds but not others (for example, compare the bowed limbs of the Cardigan Welsh corgi with the straight limbs of the Pembroke Welsh corgi). More research into this relationship would be valuable.

4.2. Chondrodystrophy

An *fgf4* retrogene in chromosome 12 results in chondrodystrophy, another phenotype characterized by shortened leg length [178]. While this mutation contributes significantly less to leg length reduction than does chondrodysplasia, it does provide additive reduction with that mutation, and is therefore at high frequency in many short-legged breeds [160]. It has additionally been found

in many breeds not considered short-legged - as many as 40 of 75 common breeds [179] - potentially due to some other phenotypic effects. Like its relative on chromosome 12, this is a gain of function mutation and therefore dominant [178].

Dogs with this mutation, in addition to mild decrease in leg length, have increased risk of intervertebral disc herniation [178,179]. Disc herniation, commonly referred to as intervertebral disc disease, is classified into type I [seen in young, chondrodystrophic dogs] and type II [seen in older, non-chondrodystrophic dogs] [180–182]. Disc degeneration occurs with age, but chondrodystrophic dogs have degeneration in nearly 100% of their discs [183]. Degeneration is seen in newborn chondrodystrophic dogs and progresses quickly, with herniation observed in chondrodystrophic dogs as young as two years of age [184]. Herniation risk is polygenic and affected by environment [185,186] as well as breed-specific genetic architecture [187]; however, it is almost always higher in dogs with the mutation [160].

Disc herniation is a significant welfare issue. It is so often acutely painful that back pain causing the dog to “scream” is strongly suggestive of this disorder; the majority of dogs are unable to walk at time of diagnosis, and 60% may be treated surgically [186] (Packer 2016). Some animals are euthanized after diagnosis or failed treatment, and even those who do well are reported to be reluctant to perform everyday activities like getting on furniture [188,189]. Chondrodystrophic dogs may have new herniations at different sites subsequent to their initial diagnosis [189,190]. At the time of diagnosis, quality of life scores for the dog average 43-47%, and owner coping scores 3/10 [191].

Disc herniation is at highest prevalence in dachshunds but varies by breed type (14-33%) [179,180,185,186,188,191,192]. Two other chondrodystrophic breeds with elevated risk are the beagle (6%) and cocker spaniel [5-6%] [180]. Other, unidentified alleles appear to contribute to variations in breed risk [179,186,187], but without breeding away from the *fgf4* chromosome 12 mutation, selective breeding can have only limited effect. The risk of disc herniation is normalized in dachshunds, which are frequently presented as dogs who should simply not be allowed to do things like jump on furniture or run down stairs [173]. The risk allele could be selectively bred out of populations with moderate to low allele frequencies. However, the question of how to remove it from breeds with high allele frequency (dachshund 94%, beagle 99%, cocker 91%) [187,193] is thorny, despite the fact that the mutation’s contribution to extreme short legs is mild to moderate.

5. Chest Depth

The ratio of thoracic width to depth is associated with risk of gastric dilatation and volvulus (GDV) [194–198]. GDV, commonly referred to as “bloat,” is the dilation and twist of the stomach, associated with significant morbidity and mortality [199,200]. While it can be seen in any dog, it is more common in large dogs (6% incidence [201]). A “deep chest” may result in a large abdominal cavity, allowing a very full stomach to stretch the hepatogastric ligament, which in turn allows the stomach to twist and cut off blood flow [198]. The risk of GDV is a complex trait, associated with many genes and environmental influences [196,198]. However, the risk is clearly higher in dogs with deeper chests; from the deepest thorax to the shallowest, the odds ratio for GDV may be 8.45 [197]. The most commonly affected breeds are German Shepherd Dogs and Great Danes [198,202]. GDV is an extremely serious diagnosis. Some affected dogs are dead by the time they reach veterinary care; many are euthanized rather than treated due to poor prognosis or financial concerns; 80-90% will survive surgery [202,203]. To mitigate this innate risk, owners may opt for preventative gastropexy, in which the stomach is sutured to the abdominal wall. Selective breeding away from the deep chest phenotype may be effective, but the German Shepherd Dog breed standard mandates a chest that “is well filled and carried well down between the legs. It is deep and capacious, never shallow” [204] and the Great Dane standard likewise mandates a “deep” chest [205].

6. Skin Folds

6.1. Facial Skin Folds in Brachycephalic Dogs

Many dogs of brachycephalic breeds have excessive skin on the face, resulting in skin folds. The skin between these folds is predisposed to skin fold dermatitis [intertrigo], or skin infections, due to the close proximity of areas of skin to each other [206,207]. For example, English bulldogs seen in primary care have 49 times the risk of developing intertrigo compared to crossbred dogs, French bulldogs 26 times the risk, and pugs 16 times the risk; these numbers may under-represent true risk factors due to underreporting of the issue, as abnormal skin may be difficult to visualize deep in folds [207]. Intertrigo may require surgical intervention to reduce the depth of folding [207]. Both owners and veterinarians may normalize excessive skin folding and struggle to recognize welfare issues associated with this morphology [145,208]. However, intertrigo causes itching, behavior change, and potentially pain, and has been named a welfare concern [206,209].

6.2. Entropion and Ectropion

Loose skin can affect ocular health, either when folds bring fur in contact with the globe (entropion) or when the lower lid everts away from the eye and fails to protect it (ectropion) [210]. Skin folds alone may obscure vision in entropion, but the contact of the fur with the globe can lead to more serious issues such as conjunctivitis, dry eye, and ulceration of the cornea, potentially eventually blindness, and may require surgical correction [211,212]. Entropion is the most common reported disorder in Shar-peis, with 18% of them affected, and is likely the root cause of the common eye problems in the breed [208], though it is seen in other breeds as well [208,211]. Eye tacking is a surgical procedure commonly used in puppies to prevent entropion and may be normalized among fanciers of this breed [213].

Inversely, when skin below the eye is too loose (ectropion), the lower eyelid cannot assist in maintenance of lubrication. Eventually the mucous tissue around the eye becomes inflamed, and chronic ocular disease may develop. Again, surgery is the treatment for severe ectropion [210]. Loose skin around the eyes is written into the Basset hound breed standard: “tight skin” is a fault, and the eyes should show a “prominent haw,” or third eyelid [176,210]. Neapolitan Mastiffs suffer from both ectropion (24% of dogs) and entropion (another 24% of dogs); 92% of dogs in this breed suffer from ophthalmologic disorders, the majority of which are related to their skin folds [214].

6.3. Shar pei Skin Folds

Two genetic mutations have been identified in association with the deep skin folds of the Shar pei. The folding and mutations are linked to Shar pei fever [a disease specific to the breed characterized by periodic bouts of fever and inflammation] and ongoing chronic inflammation [215], as well as intertrigo and ear infections [208]. This folding is considered a welfare concern in the breed [208], but the Shar Pei breed standard specifies “profuse wrinkles on the forehead continuing into side wrinkles framing the face” [216].

7. Tail Length and Curliness

7.1. Neurological Disorders

The association between tightly curled tails and neurological disorders is complex. Dogs with tightly curled tails have a high incidence of congenital vertebral malformations or CVMs [217–220]. The specific type and location of CVM, as well as type of associated neurological disorder risk, is highly breed specific [218,220]. While all tightly curled tails have historically been referred to as “screw tails,” the 2018 discovery of the DISHEVELLED 2 (DVL2) mutation clarified that the “screw tail” terminology is most appropriate for breeds such as English and French bulldogs, whose tails are both tightly curled and extremely short; the pug tail phenotype, tightly curled but normal length,

depends on a different and not yet identified mutation [219,221,222]. Additional genetic architecture may be associated with the screw-tail phenotype in bulldogs, as DVL2 does not have as strong an effect on tail phenotype in other breeds; DVL2 may also affect the brachycephaly phenotype [222], but more research is called for to assess this relationship.

In the case of both pugs and dogs of true screw-tailed breeds, CVM prevalence is extremely high, with percentages in neurologically normal French bulldogs, English bulldogs, and/or Boston terriers reported from around 50% [219,223] to around 80% [218,219,224]. CVM prevalence in pugs may be close to 100% [219]. As many dogs with CVMs are neurologically normal, veterinary opinion has historically been that the malformations are benign [218]. While pathology directly caused by CVMs appears rare, CVMs are associated with and may in fact cause spinal curvature (kyphosis) [217,224]. More extreme angles of kyphosis [over 35 degrees] are associated with neurologic deficits [225], and these deficits may be severe enough to result in non-ambulatory dogs from birth or as young as a year of age; treatment is spinal surgery which is not always successful [226,227]. Milder kyphosis is associated with spinal instability, which may increase the risk of disc herniation above or below the region of curvature [228,229] and predispose to discospondylitis, or infection of the intervertebral discs and surrounding structures [230]. French Bulldogs are particularly affected by this process; while their rates of disc herniation are somewhat lower than that of dachshunds, the average French Bulldogs herniation is on average two years earlier than the average dachshund herniation [228,231]. French Bulldogs may be at a disadvantage due to the combined effects of high prevalence of CVMs due to their screw tails, and high prevalence [91%] of the chromosome 12 FGF4 retrogene allele (associated with chondrodystrophy) [193]. Because of these associations, authors have suggested that selective breeding away from the screw-tail phenotype would be in the dogs' best interest [232].

7.2. Skin Folds Around the Tail in Screw-Tailed Dogs

Tail folds around short, curled screw tails are also associated with chronic infection [233,234]. When medical treatment fails, resolution of the problem may require partial or complete removal of the tail [233,234].

7.3. Communication

Dogs use their tails to communicate both with other dogs and with humans; emotional states and intentions conveyed by tail position and motion include threat vs appeasement or friendliness, fear or anxiety vs confidence, and excitability [235]. A comparison of canine responses to robot dogs with long versus short tails showed that dogs responded differently to long tails when they were wagging versus when they were still, but did not differentiate wagging versus still short tails - suggesting that dogs do get more information from the movements of longer tails [236]. Dogs with short tails may therefore have greater difficulty communicating than dogs with normal length tails, and additional research would be beneficial to better understand this relationship.

8. Coat

8.1. Ridge

The Rhodesian Ridgeback breed standard specifies a "ridge" along the dog's spine, which is a line of hair growing in the opposite direction to the main coat. A genome-wide association study identified the causative mutation for the ridge, a 133-kb duplication including three fibroblast growth factor genes, and also linked increasing copy number of the duplication with increasing risk of dermoid sinus [237,238]. Dermoid sinus (DS) is a developmental disorder resulting in a sinus opening running from the skin along the backbone, potentially as deep as the dura mater around the spinal cord [239]. DS can introduce infection past the skin barrier; surgical excision is the treatment of choice but may not always be curative [240,241]. DS is prevalent in Rhodesian Ridgebacks, occurring in around 5% of dogs, and breeders actively select away from it [242,243]. However, breeding away

from DS is complicated by its association with the preferred trait of having a ridge. While the mutation causing the ridge phenotype may not entirely explain the risk for DS, the risk clearly increases with increasing copy numbers of the duplicated locus [237]. Therefore, producing heterozygous dogs (who express the ridge phenotype and have decreased DS risk) may be the ideal solution, but as this involves using ridgeless dogs for breeding, there has been resistance in the breeding community [242,243].

8.2. Hairlessness

Hairlessness in the Chinese Crested (CC) is due to a mutation in FOXI3 and results in the canine ectodermal dysplasia (CED) phenotype [244]. CED is characterized by dysplastic hair follicles and numerous comedones (acne) [245]. Additionally, it is associated with a variable number of malformed, malpositioned, undersized, or entirely missing teeth [246].

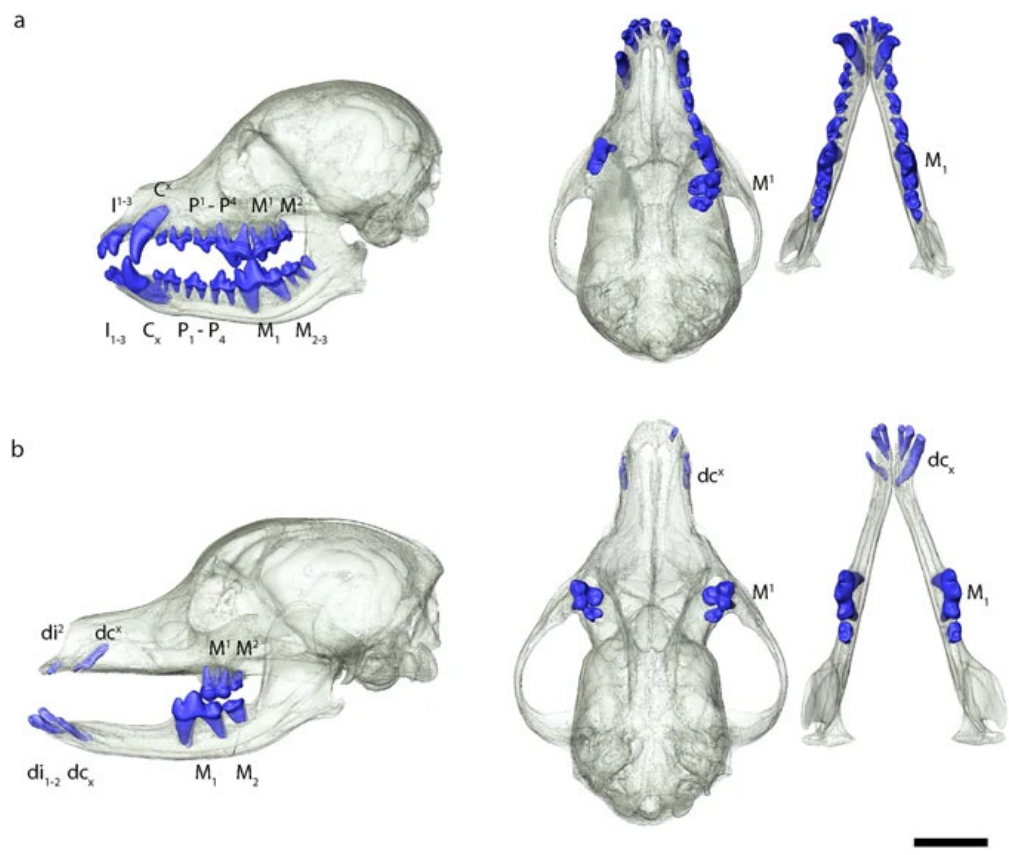


Figure 4. 3D renderings of skulls from (a) coated and (b) hairless dog [246]. Note the significant lack of teeth in the hairless dog.

8.3. Color and Pattern

A variety of coat colors and patterns are associated with disorders in the dog. Extensive white markings are associated with congenital deafness in multiple species, including in over 90 breeds of dogs [247], and are likely a problem in any breed with white coat color due to melanocyte suppression [248]. This association has been studied the most extensively in the Dalmatian, in which extreme white markings covering the entire body give the appearance of an all-white dog [the spots are controlled by a separate mutation]. A mutation in the MITF gene is associated with white markings, blue eyes, and deafness [249,250] due to a lack of cochlear melanocytes and resulting degeneration of cochlear hair cells and nerves [251]. In Dalmatians, black patches on the ears are correlated with reduced risk of deafness [251]. Nevertheless, the AKC Dalmatian breed standard notes that patches

are disqualifying [252]. About 22% of Dalmatians are unilaterally deaf, and about 8% bilaterally [and therefore clinically] deaf [251].

The Dalmatian coat is distinctive not just for its extreme white, but also for its spots. These appear to be controlled by the gene for roaning in conjunction with another, not yet identified gene to decrease the “frosted” look of a roan pattern [247,253,254]. This second, unidentified mutation is located close to (in linkage with) a mutation in SLC2A9, or may be the same mutation. The SLC2A9 mutation disrupts uric acid transport; as a result the Dalmatian breed, prior to an outcross to Pointer, was fixed for this mutation, resulting in a high risk of urinary stones [255]. The Pointer outcross produced a population of Dalmatians heterozygous or homozygous for the wild-type allele, with normal uric acid transport. However, use of these dogs is resisted by some breeders as their spots are perceived as often “frosted” [256], potentially a sign that the unidentified mutation that works epistatically with roaning to produce spots is not present, or present in altered form, in this population. Better characterization of the mutation [s] controlling Dalmatian spots may provide valuable tools to the breeding community.

Merle is another dramatic coat pattern selected for in many breeds. Heterozygous merle coats display patchy areas of dilute color; homozygous merle coats are mostly white with patches of dilute. The merle allele is a variable-length SINE insertion in the SILV gene [257–259]. Homozygous merles are at high risk of deafness [unilateral or bilateral], blindness, microphthalmia, and sterility; heterozygous merles are also at risk, though it is reduced compared to homozygotes [251,260]. Nevertheless, breeding recommendations focus on avoiding homozygous merles rather than moving away from the pattern entirely [247,259]. Meanwhile, merle is being introduced to new breeds, such as the Poodle and French Bulldog.

Several variants in the MLPH gene cause coat color to be “diluted,” for example from black to “blue” or brown to “isabella” or “fawn” [244,261–263]. Dilution has long been associated with color dilution alopecia (CDA) [264]. One of the MLPH variants (d1) is clearly associated with CDA in various breeds [265], while potential association of the other two variants (d2, d3) has yet to be investigated [247]. CDA is a dysfunction of the hair follicle, characterized by clumping of melanin and progressive hair loss [265,266]; the skin may become itchy and infected [264]. The association between dilute color and CDA varies by breed, suggesting additional genetic architecture modifying the phenotype [265]. For example, it is less common and the phenotype less extreme in Weimaraners [267], a breed in which the d1 variant is fixed. In other breeds, the association may be quite strong, for example, as high as 60% prevalence in dilute Dobermans [264]. Nevertheless, dilution variants have been recently introduced into some breeds, such as Labrador Retrievers [268], and are becoming increasingly popular in others, such as French bulldogs [269].

9. Discussion

Many common morphologies in artificially selected dogs have well-documented negative impacts on their health and welfare [270]. In this Perspective, we have summarized major health outcomes of common morphological traits under artificial selection. Additional traits were not included here due to space limitations, for example the association of pendulous ears with ear infections [271,272]; meanwhile, other traits are anecdotally linked to negative health impacts but it appears that the supporting research has not yet been done, for example, the black tongue of the Chow Chow and increased risk of oral melanoma. These negative impacts raise an important question – what does a physically sound dog look like? Free-living village dogs may offer some insight. Unlike selectively bred dogs, village dogs evolve under natural selection, which favors phenotypes that promote survival and reproduction. Consequently, village dogs may demonstrate a range of physical characteristics that are associated with robust innate health. For example, most village dogs are medium-sized (11-20 kg) irrespective of their geographic origin [273–277], suggesting that this might be an optimal body size for dogs, at least in the geo-climatic regions in which most sampling has occurred to date. However, purpose-bred dogs and village dogs generally live in

different environments, so the same physical traits may not necessarily promote health in all populations. This is an important topic for further study.

The exaggerated morphologies observed in some purpose-bred dogs, but not village dogs, are the product of modern selective breeding practices based on aesthetic preference [278]. This is exemplified by the French Bulldog, the most popular breed in the United States in 2024 [279], which exhibits several extreme traits associated with adverse health outcomes, such as airway obstruction, gastrointestinal issues, labor difficulties, skin fold infections, and vertebral disc herniation [207,228,280]. The popularity of the French Bulldog has not only increased the prevalence of extreme phenotypes, but has also helped normalize them [103]. These morphologies are frequently associated with physical discomfort and reduced functionality, and their impacts can extend beyond the specific morphology itself. For example, physical discomfort from conditions like chronic pain or severe itching has been linked to behavioral changes, including increased aggression and decreased trainability [28,281].

The accumulated evidence presented in this Perspective strongly supports the conclusion that artificial selection based on physical appearance can have substantial and often detrimental impacts on the health and welfare of purebred dogs. Many current breeding practices permit the continued propagation of harmful traits rather than actively altering breeding regimes to lessen them. To mitigate these issues, there is a pressing need to reconsider how we approach breeding practices and breed standards - as well as how to mitigate consumer demand for “exotic” dogs with extreme phenotypes. This consumer demand drives the introduction of extreme phenotypes into new breeds (such as merle coloring or hairlessness into French Bulldogs), or the further exaggeration of existing phenotypes (such as “big rope” French Bulldogs with even more extreme wrinkling).

Future directions in this field could include welfare epidemiology research to better understand the relationship between morphology, health, and behavior across different dog populations. Efforts to prioritize innate health, such as those outlined by organizations like the Brachycephalic Working Group [282], offer a promising path forward. Defining core health attributes for dogs, such as functional respiratory anatomy and sound musculoskeletal structure, could guide breeding toward healthier populations - work which depends on evidence-based assessments of when morphologies become “extreme” and thereby detrimental. Alternatives to traditional breeding practices should also be considered. These might include adjusting breed standards to prioritize health and functionality, promoting the value of mixed-breed dogs, and supporting alternative registries that emphasize both physical and behavioral wellbeing [21]. Change is possible, as demonstrated by recent adjustments to breed standards in the United Kingdom aimed at reducing harmful traits [283]. By shifting the focus from appearance to health, and by evaluating which morphologies negatively affect health, we can take meaningful steps to improve the lives of dogs [284].

10. Conclusions

In this review, we have summarized the impacts of artificially selected morphological traits on dogs’ wellbeing. It is clear that artificial selection to suit arbitrary human aesthetic preferences can result in poor outcomes for dogs’ physical and behavioral health. Notably, many of these breeding practices do not include selection for the niche in which dogs now live - inside human households - which is very different from their niche even 100 years ago.

While lineages of dogs have differed in morphological phenotype for many hundreds of years, strong, intensive, intentional selection for traits related to appearance began in earnest during the Victorian era. At that time, the health consequences of selection on these traits were not well understood. Now they are, and we have a responsibility to the animals we breed to take their welfare into consideration.

In this Perspective, we have only skimmed the surface of each of the covered traits. Our aim is to create a basis for future work that can delve more deeply. Two fundamental needs are apparent: first, to better research and understand the mechanisms and etiologies of health outcomes of morphological selection; and second, to enact changes in breeding practices. If we can define clear

guidelines for when extreme morphology becomes a welfare issue, this can support evidence-based efforts to set new breeding goals. How should we determine the boundary between morphologies that do and do not have substantial impairment on innate health? How should physiological and health data be gathered and interpreted to guide breeding practices? How can members of the general public be informed about the ethical consequences of their financial support for particular selection regimes?

The researchers listed below have added their names to those of the article's authors in calling for the scientific and veterinary communities - and the general public - to consider these issues.

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