The association between coat phenotype and morphology conducive to high running speeds in *canis lupus familiaris*

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Abstract

The mechanics of animal locomotion has fascinated man for centuries. In particular, we have sought to understand why certain species are able to reach such prodigious running speeds (perhaps due to our woeful inadequacy in this area (Bramble & Lieberman, 2004)**). Such investigations have focused on the role that functional anatomy and morphology play in facilitating the attainment of high running speeds** (Williams, Payne & Wilson, 2007; Hudson et al., 2011). ***Canis lupus familiaris*, or the domestic dog, serves as an excellent model for such investigations due to the great variation in running speeds exhibited across breeds, and there is a dense body of literature that has considered how the anatomy of certain canines has been adapted to the task of high speed running. Similarly, a great deal is known about the dog genome, and thus adaptations that are thought to be advantageous in the context of sprinting can be linked to their genetic basis** (Mosher et al., 2007). **Aerodynamics is one aspect of morphology that is known to be important for high speed running** (Lull, 1904)**, yet despite this, the association between a dog's coat phenotype and the ability to run fast has not been determined. This omission is surprising given the influence of the surface properties of a body on its aerodynamics. Here I use the breed definitions of the American Kennel Club** (American Kennel Club, 1998)**, to show, graphically, statistically and in prose, by reference to previous literature** (Cadieu et al., 2009)**, and by using the mass/height ratio to indicate morphological adaptations for high speed running, that within the larger dog breeds (and in particular within breeds that are known for their running ability** (Fischer & Lilje, 2011)**), there is no association between coat phenotype and other morphological adaptations that are known to be conducive to high speed running (τ_B = -0.23, p = 0.04).**

The study of animal locomotion has a rich and vibrant history that often attracts a great deal of public attention. For instance, the photographic studies (Muybridge, 1883, 1893) of Eadweard Muybridge (a hirsute gentleman born within barking distance of our university) are as popular as he was notorious (Clegg, 2007). Despite this interest, and the research that has sprung from it, our understanding of the way in which animal morphology facilitates movement is far from complete and there are a number of heavily debated issues and bones of contention. The purpose of this study was to address a surprising omission within the literature by considering the influence of an animal's coat on their ability to move at high speed.

The domestic dog is a unique model for studying the adaptations of an organism to its function and environment. Years of rigorous selective breeding mean that there is more morphological variation within the dog family than for any other carnivore (Wayne & vonHoldt, 2012). Similarly, dogs have been bred to perform a variety of functions, across a spectrum from working and racing to loafing and handbag dwelling. The dog model therefore represents an unrivalled opportunity to study the way in which the morphology of an animal is adapted to its function. Similarly, the canine model is highly useful in relating differences in morphology and behaviour to genetics (Wayne & Ostrander, 2007; Parker, Shearin & Ostrander, 2010).

There is a great range in the top speeds of different members of the dog family, with certain breeds being among the fastest of land animals (that is, among the top dogs). Consequently, the canine model is particularly useful for understanding how the morphology of an animal can be adapted to facilitate the attainment of high running speeds. For instance, the greyhound (a dog capable of reaching speeds of over 60 km/h (Usherwood & Wilson, 2005)) has been an attractive choice (fancied?) for biomechanists interested in the kinematics and kinetics of locomotion (Jayes & Alexander, 1982; Usherwood & Wilson, 2005; Williams et al., 2009; Angle, Gillette & Weimar, 2012) and the functional anatomy involved in such performances (Williams et al., 2008; Webster, Hudson & Channon, 2014) (it should be noted that the popularity of greyhound racing may provide a pecuniary motivation for this work). Similarly, in recent years the canine model has been a productive workhorse for groups interested in identifying the genetic basis of morphological traits thought to facilitate or be indicative of the ability to run at high speed. These include body mass, size and limb length (Sutter et al., 2007; Boyko et al., 2010; Rimbault et al., 2013), increased muscle mass (Mosher et al., 2007) and skull shape (Schoenebeck et al., 2012).

One factor that has not been investigated is the impact of a dog's coat on their speed of locomotion. This is surprising given the impact of a body's surface properties on its aerodynamics (through a range of mediums). Given the importance of aerodynamics (Lull, 1904) at the types of speeds that the fastest dogs achieve it seems likely that such dogs will have short coats that create minimal wind resistance. Thus I hypothesized that there would be an association between coat phenotype and high running speed, with faster dogs having shorter coats and slower dogs having longer, thicker and generally shaggier coats.

It has been previously demonstrated that a dog's coat phenotype is governed by only 3 genes (Cadieu et al., 2009). Consequently, if a link between coat phenotype and high running speed could be established common sense suggests that this would signal new candidate genes that explain athletic performance. Such a finding is of importance given the rarity of such discoveries (Mosher et al., 2007) and the potential ramifications for the understanding of human medicine and performance (for instance, such a link would explain the high rate of baldness (another aerodynamic adaptation) within elite male sprinters – a phenomenon of both medical and sporting importance).

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In this work, I used the classification of coat phenotype provided by Cadieu and colleagues (Cadieu et al., 2009) in order to quantify the relative thickness of coat of the breeds considered (a larger number being indicative of a less aerodynamic coat). The literature describing the maximum velocity of canine locomotion is sparse, making the quantification of the running velocity of each breed a more knotty problem, however, I was dogged in my search for solution. In the end I settled on the use of the mass/height ratio as a proxy to describe morphometry that is conducive to high speed running. This approach is based on the premise that a relatively lighter body mass with relatively longer legs is an adaptation that permits the achievement of greater running velocity (Parker & Ostrander, 2005) (an assumption which I believe has legs). In addition, I compared the characteristics of the sight hounds (a group of dogs defined by their adaptation for high speed running (Fischer & Lilje, 2011)) to the wider population, hypothesizing that the coats of these breeds would be adapted for high speed running. Finally, I restricted this study to larger dog breeds (above 20 kg) as efficiency of locomotion does not seem to have been a trait that has been desired by fanciers of the lap dog. Examples of the breeds considered in this study are presented in Figure 1.

Figure 1. Examples of the variation in coat phenotype and mass/height (M/H) ratio for the breeds considered in this study. The dogs in the first row are all sight hounds, a group defined by its adaptations for high speed running (Fischer & Lilje, 2011). The dogs in the second row are other breeds not thought to be adapted for feats of great running speed.

In reporting the results of this study, I was keen to emulate the concision of Dennis Upper's (Upper, 1974) seminal work in applied behavioural analysis, as this approach leads to an exemplary clarity of message (not least by eliminating arguments that are too woolly). In addition, staying up to date with the academic literature is a Sisphyean task (I for one am constantly chasing my tail), and the last thing I wanted to do was to waste anyone's time. To this end, the statement of results and their interpretation is cut intentionally short. Firstly,

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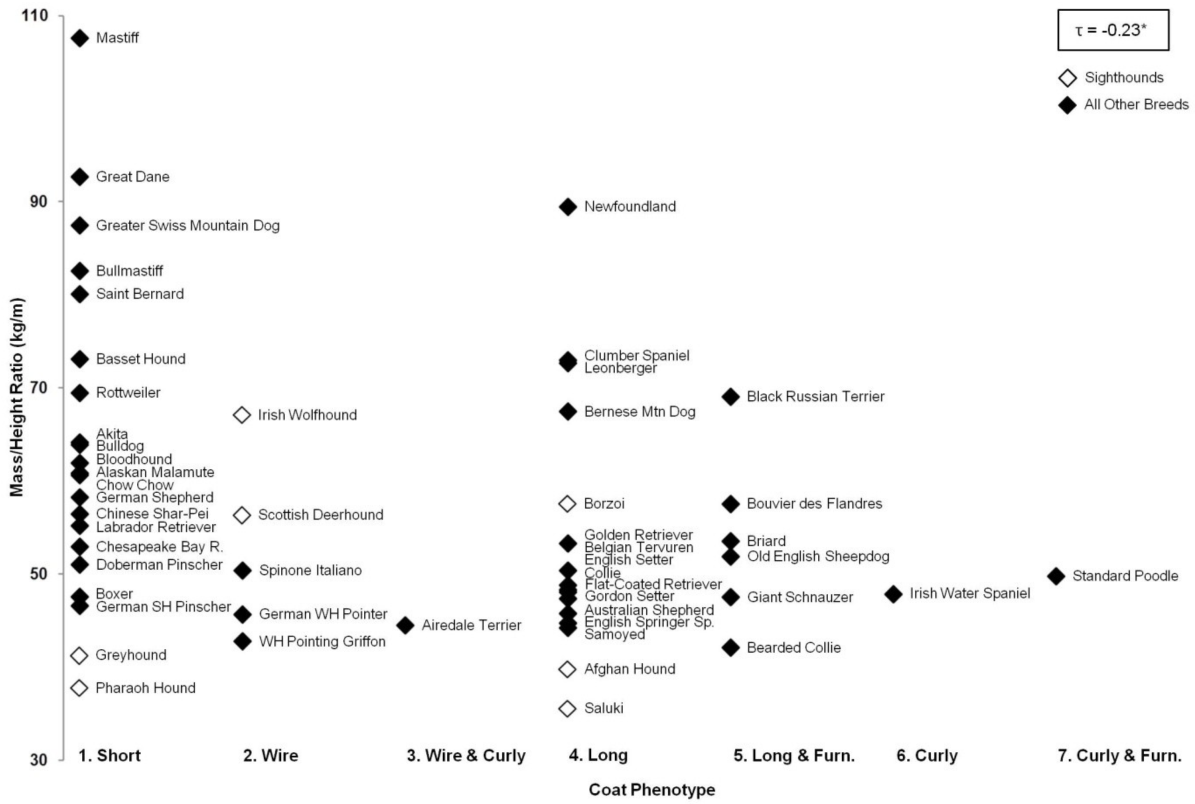
there was no association between coat phenotype and mass/height ratio (τ_B = -0.23, p = 0.04; Figure 2). Secondly, the distribution of coat phenotypes among the sight hounds was not different to that of the other breeds (χ^2 (6) = 5.00, p = 0.54). These findings may indicate that there is no association between coat phenotype and morphology conducive to high speed running and that to make such a suggestion is barking up the wrong tree. Although it might seem far-fetched, Occam's Razor seems to suggest that there may be other factors that explain the variation in coat phenotype within the dog kingdom (although it seems to me that a credible alternative explanation is that contemporary statistical tools lack the power to establish such an association).

Figure 2. The association between coat phenotype and morphology conducive to high speed running in 51 larger dog breeds. The mass/height ratio (y-axis) is used as a proxy for morphology conducive to high speed running (smaller values indicating a greater adaptation for high speed running). Breeds that lie towards the right of the figure are increasingly shaggy.



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Author Information The author declares that he has no competing financial interests, although he does confess to an understandable antipathy towards the owners of lap dogs. Correspondence and requests for materials should be addressed to the author (daniel.cleather@stmarys.ac.uk).