

RESEARCH ARTICLE

Comparative locomotor costs of domestic dogs reveal energetic economy of wolf-like breeds

Caleb M. Bryce* and Terrie M. Williams

ABSTRACT

The broad diversity in morphology and geographic distribution of the 35 free-ranging members of the family *Canidae* is only rivaled by that of the domesticated dog, *Canis lupus familiaris*. Considered to be among nature's most elite endurance athletes, both domestic and wild canids provide a unique opportunity to examine the variability in mammalian aerobic exercise performance and energy expenditure. To determine the potential effects of domestication and selective breeding on locomotor gait and economy in canids, we measured the kinematics and mass-specific metabolism of three large (>20 kg) dog breed groups (northern breeds, retrievers and hounds) of varying morphological and genomic relatedness to their shared progenitor, the gray wolf. By measuring all individuals moving in preferred steady-state gaits along a level transect and on a treadmill, we found distinct biomechanical, kinematic and energetic patterns for each breed group. While all groups exhibited reduced total cost of transport (COT) at faster speeds, the total COT and net COT during trotting and galloping were significantly lower for northern breed dogs (3.0 and 2.1 J kg⁻¹ m⁻¹, respectively) relative to hound (4.2 and 3.4 J kg⁻¹ m⁻¹, respectively) and retriever dogs (3.8 and 3.0 J kg⁻¹ m⁻¹, respectively) of comparable mass. Similarly, northern breeds expended less energy per stride (3.5 J kg⁻¹ stride⁻¹) than hounds or retrievers (5.0 and 4.0 J kg⁻¹ stride⁻¹, respectively). These results suggest that, in addition to their close genetic and morphological ties to gray wolves, northern breed dogs have retained highly cursorial kinematic and physiological traits that promote economical movement across the landscape.

KEY WORDS: Canids, Gait, Kinematics, Locomotion, Metabolism**INTRODUCTION**

All domestic dogs (*Canis lupus familiaris*) are recent and exclusive decedents of gray wolves, *Canis lupus* Linnaeus 1758, having been domesticated in the last 15,000–30,000 years (Freedman et al., 2014; Skoglund et al., 2015; Wang et al., 2016). However, among the nearly 400 breeds representing modern dogs (Kleiman et al., 2003), unique artificial selection trajectories (Galibert et al., 2011; Jimenez, 2016) have resulted in extreme morphological diversity that exceeds that for the remainder of the family *Canidae* (Clutton-Brock, 1999; Lindblad-Toh et al., 2005; Vaysse et al., 2011; Wayne, 1986, 2001; Wilcox and Walkowicz, 1995). In recent years, much emphasis has been placed on elucidating the origins of dog domestication from genomic (e.g. Freedman et al., 2014; Parker, 2012; Skoglund et al., 2015; Vonholdt et al., 2010) to

zoarcheological (Perri, 2016; Pionnier-Capitan et al., 2011), morphometric (Drake et al., 2015) and biogeographical evidence (Larson et al., 2012). By comparison, little is known about the effects of extensive artificial selection on physiological performance and metabolic demands of the different breeds of dog (but see Bermingham et al., 2014; Careau et al., 2010; Speakman et al., 2003).

With the highest sustained metabolic rates on record (approximately 4400 J kg⁻¹ day⁻¹ while racing 490 km in 3 days at approximately -20°C; Hinchcliff et al., 1997), canids are considered among the most elite endurance athletes in the natural world (Miller et al., 2015; Poole and Erickson, 2011; Snow, 1985). This compares with approximately 3900 J kg⁻¹ day⁻¹ for lactating mice raising artificially large litters (14 pups) in a cold environment (5°C; Hammond et al., 1994), 2000 J kg⁻¹ day⁻¹ for thoroughbred horses during heavy training (Lewis, 1995; Pagan and Hintz, 1986) and 1400 J kg⁻¹ day⁻¹ for Tour de France cyclists (Westerterp et al., 1986). Dogs, coyotes, wolves and foxes exhibit aerobic performance capacities roughly three times greater than those of equivalently sized terrestrial mammals (Seeherman et al., 1981; Taylor et al., 1987a; Weibel and Hoppeler, 2005; Weibel et al., 1983, 2004). Dogs, for example, have aerobic scopes [the ratio of maximum oxygen uptake ($\dot{V}_{O_{2,max}}$) to basal metabolic rate] of 20–30, compared with aerobic scopes of about 10 for goats of equal body mass (Weibel et al., 1987). To facilitate this greater oxygen capacity, dogs possess structural and functional adaptations at each step in the pathway for oxygen, including in the muscle mitochondria, muscle microvasculature, heart and lungs (reviewed in Taylor et al., 1987b). Together, the wide aerobic scopes exhibited by canids are consistent with an ability to run for extended periods at sustained speeds without becoming anaerobic (Koteja, 1987; Okarma and Koteja, 1987).

Given these physiological and morphological characteristics, both domestic and wild canids provide a unique opportunity to investigate mammalian exercise performance and energy expenditure. The expectation is that aerobic capacity provides a selective advantage for wild canids (Okarma and Koteja, 1987). In the wild, the rates at which individuals acquire, transform and expend energy (i.e. their metabolic rates) are integrative measures of organism function that have fundamental consequences for survival and reproductive success (Brown et al., 2004; Halsey, 2011). For many highly mobile species such as canids, the energetic costs associated with activity and movement form a substantial portion of daily energy expenditure (Boisclair and Leggett, 1989; Garland, 1983; Girard, 2001; Gorman et al., 1998; Karasov, 1992; Rezende et al., 2009; Scantlebury et al., 2014; Tatner and Bryant, 1986; Weibel et al., 2004). In wolves and dogs, movement costs are superimposed on elevated energy demands associated with large body size (Peters, 1983), endothermy (Bennett and Ruben, 1979) and carnivory (Carbone et al., 2007, 2011), suggesting a key selective advantage for minimizing locomotor costs.

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List of symbols and abbreviations

CoM	center of mass
COT	cost of transport ($\text{J kg}^{-1} \text{m}^{-1}$)
COT _{net}	net cost of transport ($\text{J kg}^{-1} \text{m}^{-1}$)
COT _{tot}	total cost of transport ($\text{J kg}^{-1} \text{m}^{-1}$)
RMR	resting metabolic rate ($\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$)
t_c	foot contact time (s)
\dot{V}_{O_2}	rate of oxygen consumption ($\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$)

Here, we examined how selective breeding and domestication may have disrupted the optimization of these locomotor costs and altered the economy of movement in domestic dogs. This was accomplished by comparing the locomotor kinematics and energetics of three large (>20 kg) breed groups along a continuum of relative genetic and morphological proximity to gray wolves. Northern breed individuals included Siberian huskies, Alaskan malamutes and Samoyeds. These ‘sled dogs’ are among the oldest domestic dog breeds (Huson et al., 2010; Parker, 2012; Wang et al., 2013) and possess the most lupine traits (i.e. bear the greatest morphological and genomic resemblance to their wild progenitor, the gray wolf; Mech, 1970; Parker et al., 2004; Skoglund et al., 2015; Udell et al., 2010; Vonholdt et al., 2010). Northern breeds have been traditionally used to assist humans with long-distance activities including arctic hunting expeditions and sledge pulling (Rennick, 1987). Scent hounds, such as the Plott hounds measured in the present study, were primarily bred to aid hunters by tracking the scent of wild game (American Kennel Club, 2006), an activity that requires speed but only intermediate levels of aerobic endurance relative to northern breeds. Retrievers (e.g. golden, labrador, flat-coated) were also bred to assist in hunting, but typically require shorter, largely anaerobic bouts of activity to retrieve killed or injured game (American Kennel Club, 2006). Because the genomic and morphological effects of dog domestication have been described (e.g. Drake et al., 2015; Freedman et al., 2014; Parker, 2012; Skoglund et al., 2015), our goal was to assess the coincident energetic consequences of human-induced selective pressures for various physical traits (e.g. limb length, body mass) and desired tasks (e.g. guarding, hunting, pulling loads). We found that working breeds of dogs most similar to wolves (i.e. northern breeds) have lower metabolic transport costs than hounds and retrievers, which have undergone divergent artificial selection trajectories from this wild canid progenitor.

MATERIALS AND METHODS**Study design**

We quantified the overground stride mechanics, kinematics and preferred speeds of steady-state walking, trotting and galloping in three breed groups of domestic dogs differing in genomic relatedness to the gray wolf. These data were then paired to the gait-specific metabolic demands of level exercise for these animals measured by open-flow respirometry. Metabolic rates across each gait, total and net cost of transport, as well as the cost per stride were used to compare overall locomotor energy economy across the dog breeds. Assuming that the genetic distance from wolves approximates the relative extent of domestication (Parker, 2012), we then used the breed-specific data to assess the potential effect of increased domestication on the economy of movement in dogs.

Table 1. Summary of morphological characteristics for the dogs examined in this study

Breed	Sample (N: m,f)	Mass (kg)	Age (years)	Forelimb length (m)	Hindlimb length (m)
Northern	9: 4,5	33.1±3.8	5.9±1.1	0.59±0.03	0.56±0.03
Hound	7: 6,1	24.2±0.9	6.0±1.2	0.49±0.02	0.5±0.02
Retriever	7: 5,2	33.2±2.3	5.4±1.2	0.6±0.04	0.61±0.05

Data are means±s.e.m. No characteristics differed significantly ($P<0.05$) across breeds.

Animals

The study consisted of 23 healthy, adult dogs (2–11 years old) in three breed categories: northern breeds ($N=9$), hounds ($N=7$) and retrievers ($N=7$; Table 1).

All dogs were deemed healthy, active and without any known impairments that might influence locomotion. To ensure adequate conditioning and mitigate training effects associated with the study protocol, all subjects participated in routine outdoor exercise and were physically trained for at least 1 month prior to and throughout data collection. Informed written consent, animal age and health history were obtained from all dog owners, and the study protocol was approved by the UC Santa Cruz Institutional Animal Care and Use Committee.

Gait mechanics and kinematic data

To determine the physiological basis of gait selection and preferred performance parameters (Kar et al., 2003; Nanua and Waldron, 1995; Perry et al., 1988), we analyzed the natural, unrestrained locomotor gaits of each dog with repeated outdoor kinematic trials. During each trial, dogs walked, trotted and galloped at steady-state speed along a 10 m transect of level ground while being filmed by high-speed (Casio EX-F1, 300 frames s^{-1}) and high-definition (Sony HDR-CX290/B, 1080 HD, 60p) video cameras mounted perpendicular to the test course and in the dog’s cranial–caudal sagittal plane.

Videos were analyzed (Corel VideoStudio ProX5, Ottawa, ON, Canada) for animal speed and basic stride mechanics (stride length, stride frequency). Given the dynamic and geometric similarity of the subjects (Alexander, 1984, 2005; Alexander and Jayes, 1983), dimensionless Froude numbers ($\text{speed}^2/\text{limb length} \times \text{gravitational acceleration}$) were computed for gait transitions to compare breeds after accounting for limb length. We excluded from analysis all passes in which the dog visibly changed gait or speed mid-transect, turned its head, or otherwise deviated from a straight-line path. The preferred range of speeds for each gait was then calculated for each animal and used to ensure that subsequent metabolic treadmill trials approximated the preferred walking, trotting and galloping speeds of the individual dog.

Previous studies report that, overall, dog sagittal-plane gait patterns on a level treadmill do not differ from those of overground locomotion (Torres et al., 2013), although the stance phase is slightly longer (Fischer and Lilje, 2011). We tested these findings, and closely examined gait kinematic differences across breeds, using a random subset of at least four dogs within each breed group. Anatomical landmarks on the limb joints were determined via manual palpation while flexing and extending each joint, then digitized and tracked at 300 Hz from high-speed videos (Tracker Video Analysis and Modeling Tool, <http://physlets.org/tracker/>) to measure 24 biomechanical and kinematic parameters (Table 2; Table S1) from the subjects moving overground and on the treadmill at the same gait and speed ($\pm 10\%$).

Table 2. Kinematic parameters of each gait for northern breed, hound and retriever groups (N=4 for each group)

	Walk			Trot			Gallop		
	Northern	Hound	Retriever	Northern	Hound	Hound	Northern	Hound	Retriever
Forelimb									
Protraction length* (m)	0.547 ^a	0.484 ^a	0.479 ^a	0.591 ^a	0.499 ^a	0.579 ^a	0.811 ^a	0.39 ^b	0.548 ^{a,b}
Protraction angle (deg)	28.4 ^a	24.4 ^a	26.7 ^a	30.7 ^a	29.5 ^a	27.5 ^a	34.11 ^a	42.7 ^a	39.0 ^a
Retraction length* (m)	0.305 ^a	0.445 ^a	0.362 ^a	0.401 ^{a,b}	0.551 ^a	0.322 ^b	0.505 ^a	0.593 ^a	0.44 ^a
Retraction angle (deg)	15.7 ^a	20.8 ^a	19.5 ^a	17.9 ^a	25.6 ^b	16.5 ^a	23.57 ^a	28.63 ^a	21.48 ^a
Stride duration (s)	0.807 ^a	0.912 ^a	0.799 ^a	0.52 ^a	0.469 ^a	0.529 ^a	0.413 ^a	0.394 ^a	0.442 ^a
Swing phase duration (s)	0.309 ^a	0.323 ^a	0.34 ^a	0.274 ^a	0.246 ^a	0.277 ^a	0.247 ^a	0.273 ^{a,b}	0.35 ^b
<i>t_c</i> (s)	0.498 ^a	0.589 ^a	0.458 ^a	0.247 ^a	0.223 ^a	0.252 ^a	0.166 ^a	0.121 ^b	0.092 ^b
Hindlimb									
Protraction length* (m)	0.34 ^a	0.362 ^a	0.33 ^a	0.337 ^a	0.287 ^a	0.356 ^a	0.444 ^a	0.38 ^a	0.37 ^a
Protraction angle (deg)	17.7 ^a	13.9 ^a	18.8 ^a	16.8 ^a	17.3 ^a	17.3 ^a	20.08 ^a	20.67 ^a	19.55 ^a
Retraction length* (m)	0.588 ^a	0.608 ^a	0.474 ^a	0.573 ^a	0.667 ^a	0.547 ^a	0.729 ^a	0.342 ^a	0.597 ^a
Retraction angle (deg)	28.2 ^a	23.8 ^a	26.2 ^a	26.7 ^a	31.1 ^a	26.8 ^a	36.43 ^a	46.07 ^a	31.17 ^a
Stride duration (s)	0.804 ^a	0.909 ^a	0.79 ^a	0.533 ^a	0.472 ^a	0.515 ^a	0.413 ^a	0.379 ^a	0.433 ^a
Swing phase duration (s)	0.294 ^a	0.321 ^a	0.313 ^a	0.27 ^a	0.262 ^a	0.28 ^a	0.325 ^a	0.266 ^a	0.248 ^a
<i>t_c</i> (s)	0.509 ^a	0.588 ^a	0.478 ^a	0.263 ^a	0.211 ^a	0.235 ^a	0.165 ^a	0.113 ^a	0.108 ^a
Other									
Head angle (deg)	169.3 ^a	160.3 ^a	166.5 ^a	165.3 ^a	173.4 ^a	165.0 ^a	166.22 ^a	157.28 ^a	166.34 ^a
Vertical displacement (cm)	5.23 ^a	1.71 ^b	2.71 ^{a,b}	4.51 ^a	3.62 ^a	3.96 ^a	5.6 ^a	7.5 ^{a,b}	11.66 ^b

t_c, contact time, representing stance phase duration.

Intergroup means not connected by a common letter differ statistically ($P < 0.05$).

*Indicates relative linear measurement (normalized by forelimb or hindlimb length of the individual dog) for direct comparison.

Metabolic measurements and energetic costs

Because animals change gaits to achieve stability and minimize energetic costs of movement (Biewener, 1990; Cavagna and Kaneko, 1977; Hoyt and Taylor, 1981; Hoyt et al., 2006), we compared gait-specific metabolic demands across breed groups. We took simultaneous kinematic and metabolic measurements during level treadmill running for a subset of dogs according to Williams et al. (2002). For each dog, the rate of oxygen consumption (\dot{V}_{O_2} , ml O₂ kg⁻¹ min⁻¹) during rest and each gait was measured by an integrated open-flow respirometry system (TurboFOX-RM, Sable Systems International, Las Vegas, NV, USA). Following an overnight fast to ensure post-absorptive state, each animal was conditioned to rest (standing stationary or lying still in sternal recumbency), walk, trot and gallop inside a reinforced Plexiglas metabolic chamber (1.6 m × 0.5 m × 1 m) mounted on the surface of a variable-speed treadmill (Q65, Quinton Instrument Co., Bothell, WA, USA). The chamber was equipped with a fan to facilitate rapid mixing of expired gas and prevent overheating of exercising dogs. Each dog was weighed (Aryln 320D, East Rockaway, NY, USA) prior to every exercise trial, and air temperatures averaged 23.4°C (range 22–25°C) within the chamber during measurements. These temperatures fell within the thermoneutral zones of these breeds (National Research Council, 2006; Speakman et al., 2003). To ensure that the animals reached a physiologically stable state, each randomized exercise trial lasted a minimum of 12 min; sessions that included a pre-exercise resting metabolic rate (RMR) measurement lasted approximately 25 min.

Chamber air was drawn through the system with an integrated vacuum pump at a flow rate of 230 l min⁻¹. At this flow rate, the fractional concentration of oxygen in the chamber remained above 0.2040 to avoid hypoxic conditions. Sub-samples of air from the exhaust port of the chamber were drawn through a series of six columns, alternatingly filled with desiccant (Drierite, W. A. Hammond Drierite, Xenia, OH, USA) and CO₂ scrubber (Sodasorb, W.R. Grace & Co, Chicago, IL, USA) before entering an oxygen analyzer. The main flow rate through the chamber, percentage of oxygen in the expired air, humidity of the gas sample and barometric pressure were monitored continuously and recorded

once per second on a computer using Expedata software (Sable Systems International). All values were corrected to standard temperature and pressure, dry (STPD), and the entire system was calibrated daily with ambient air (20.95% O₂ at sea level where trials occurred) and with dry N₂ gas to test for chamber mixing and leaks according to Fedak et al. (1981).

For each trial, average \dot{V}_{O_2} was calculated using eqn 4b from Withers (1977) and an assumed respiratory quotient of 0.82 for dogs consuming a conventional, mixed diet (Raab et al., 1976; Speakman et al., 2003). Physiological measurements, including energetic cost per kilogram per unit distance (cost of transport, COT; J kg⁻¹ m⁻¹) and cost per stride (J kg⁻¹ stride⁻¹), were derived from speed and stride frequency, respectively, using an energy conversion of 20.1 J ml⁻¹ O₂, assuming a negligible contribution from anaerobic glycolysis (Schmidt-Nielsen, 1997; Taylor et al., 1982). Total cost of transport (COT_{tot}) was derived from the slope of the energy expenditure–speed relationship for each breed, i.e. COT_{tot} was calculated for each trial measurement by dividing mass-specific metabolic cost by the trial speed. Net cost of transport (COT_{net}) was calculated by subtracting the mean RMR of each individual from the energetic cost of the trial, then dividing by trial speed. Both COT_{tot} and COT_{net} include any postural costs during locomotion (the difference between mean RMR and the *y*-intercept in the energy expenditure–speed relationship; Halsey, 2013, 2016).

During the metabolic measurements on the treadmill, we recorded stride length and stride frequency using high-speed and high-definition cameras (described above) mounted in the sagittal plane on the right side of each dog at a distance of 1.65 m. The timing intervals for sequential cycles of the right forelimb were averaged from the video sequences, and the number of strides taken per second was calculated for each gait (Williams et al., 2002).

Statistical analysis

Statistical analyses and figures were produced using JMP Pro12 (SAS Institute Inc., Cary, NC, USA) and R (v. 3.1.1, <https://www.r-project.org/>). We used principle components analysis (PCA) and linear discriminant analysis (LDA) in tandem to compare kinematic

parameters across breed groups while controlling for locomotor gait. To determine the potential effect of the treadmill on kinematics, we performed paired Student's *t*-tests (two-tailed) comparing the stride frequency and stride length for treadmill and overground locomotion within the same individual and breed group. Differences in age (years), body mass (kg) and limb length (m) between groups were determined by one-way analysis of variance (ANOVA) followed by Tukey–Kramer honest significant difference (HSD) tests. We also used ANOVA with HSD to compare mass-specific \dot{V}_{O_2} and stride mechanics by gait across groups. Predicted (Heglund and Taylor, 1988) and measured preferred speeds for each gait, and transitions between gaits, were compared using paired Student's *t*-tests. We used analysis of covariance (ANCOVA) and least square linear regressions to determine the relationships between running speed and mass-specific metabolic rate, stride frequency and stride length for each individual and breed group. For all linear models, we checked the assumptions of linearity, normality and homoscedasticity by visual inspection of plotted residuals. To examine differences in metabolic COT across breeds, we fitted a three-parameter exponential decay model and determined whether 95% confidence intervals for each breed group overlapped with the estimates of the other two groups. All model combinations were fitted with best model fits based on the lowest Akaike information criteria corrected for small sample size (AICc), and study results are expressed as the mean±s.e.m. ($\alpha=0.05$, *a priori*).

RESULTS

Gait mechanics

Dog breed groups did not differ significantly from one another in age ($F_{2,20}=0.07$, $P=0.93$), body mass ($F_{2,20}=3.0$, $P=0.07$), forelimb length (i.e. withers or shoulder height above ground; $F_{2,17}=3.18$, $P=0.07$) or hindlimb length (hip height above ground; $F_{2,17}=2.81$, $P=0.09$; Table 1). However, dog breed groups differed significantly in several of the basic overground stride mechanics measured (Table S2). For example, there was wide variation in the range of speeds selected for each gait (walk, trot and gallop) across breed groups (Fig. 1; Table S2). Relative to hounds, northern breeds walked, trotted and galloped over a broader range of speeds. Retrievers showed a contracted speed range for trotting but the largest breadth of galloping speeds. According to the average travel speed for each gait, the three breed groups did not differ from one another while walking ($F_{2,134}=0.28$, $P=0.76$), but did for faster gaits (Table S2). Retrievers trotted at significantly faster

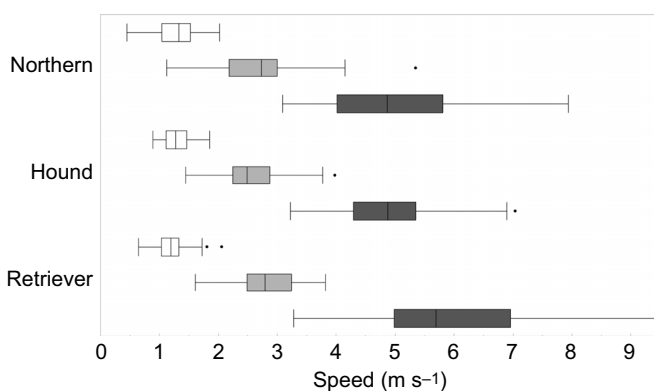


Fig. 1. Variation in the range of speeds selected for walking, trotting and galloping by northern breed, hound and retriever dogs. Box-and-whisker plots depict group-wide speed ranges (walking, white; trotting, gray; galloping, black), with the median denoted as the vertical line within each gait range quartile box. Outliers are depicted as individual points beyond the associated quartiles.

speeds than hounds ($t_{119}=1.97$, $P=0.01$) but not northern breeds ($t_{168}=1.97$, $P=0.13$). Furthermore, mean galloping speed was faster for retrievers than for both hounds and northern breeds ($F_{2,211}=17.83$, $P<0.001$; Table S2). Across groups, walk–trot transition speeds ($F_{2,20}=0.22$, $P=0.81$) and Froude numbers ($F_{2,18}=1.1$, $P=0.36$) did not differ across groups, indicating locomotor similarity at slow speeds. However, at the physiologically equivalent transition from trotting to galloping (Taylor et al., 1982), retrievers ran at faster speeds ($F_{2,20}=4.19$, $P=0.03$) and with higher Froude numbers ($F_{2,17}=5.27$, $P=0.02$) than did northern breeds or hounds.

Hounds ($t_6=5.02$, $P<0.01$) and retrievers ($t_6=2.56$, $P=0.04$), but not northern breeds ($t_6=1.4$, $P=0.2$), trotted at speeds significantly faster than predicted for quadrupeds of similar body mass (Heglund and Taylor, 1988). Hounds and retrievers also transitioned from trot to gallop at speeds that were faster than predicted by body mass (18–26% faster, $P<0.01$; Fig. 2). Only retrievers exhibited preferred

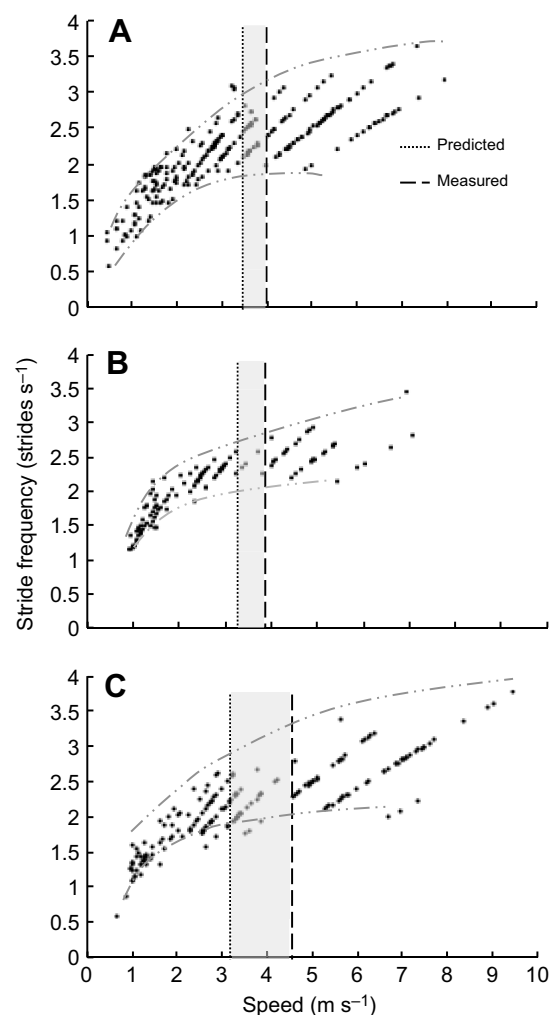


Fig. 2. Comparison of predicted and measured physiologically equivalent trot–gallop transition speeds. (A) Northern breed, (B) hound and (C) retriever dogs. The figure shows stride frequency in relation to locomotor speed while moving on a level outdoor transect. Each data point is a single measurement for a test run by an individual dog. Dash–dot lines represent the minimum and maximum range of the data across speeds. The gray box denotes the difference between measured (dashed vertical line) and predicted (dotted vertical line) (Heglund and Taylor, 1988) trot–gallop transition speeds for each breed. Pseudo-linearity of data within each group is caused by limited variation of speed–stride frequency measurements resulting from the 10 m outdoor transect length used during data collection.

galloping speeds faster than those predicted by Heglund and Taylor (1988) ($t_6=2.83$, $P=0.03$).

Kinematics

After controlling for individual, gait and speed, we found no consistent effect of the treadmill relative to overground locomotion on sagittal plane joint flexion and extension (Torres et al., 2013) and therefore assumed treadmill trials were representative of free-ranging dog locomotion. While not significantly different ($P=0.07$ – 0.09 range), limb lengths were generally shorter in hounds than in other breeds (Table 1). To account for this, we used relative limb protraction and retraction length values (dividing by limb length of each dog) in subsequent analyses (Table 2). After using PCA and LDA to condense the initial set of 24 measured kinematic parameters down to 18 variables loaded onto 5 factors as determined by eigenvalues >1 , we detected group-wide differences in trotting (Wilk's $\lambda=0.002$, $P=0.038$), but not walking (Wilk's $\lambda=0.042$, $P=0.88$) or galloping (Wilk's $\lambda=0.002$, $P=0.35$). Upon closer analysis of each gait with ANOVA, we found that, relative to hounds and retrievers, northern breeds had the greatest vertical displacement while walking (5.2 ± 1.4 cm, $F_{2,17}=5.0$, $P=0.02$), and that this displacement exceeded that of their trot (4.5 ± 0.9 cm; Table 2). While trotting, forelimb retraction length was greater in hounds than in retrievers ($t_{13}=2.1$, $P<0.01$), and forelimb retraction angle was greatest in hounds relative to both other groups ($F_{2,18}=10.54$, $P<0.01$; Table 2). During gallop, northern breeds showed longer forelimb stance durations ($F_{2,10}=17.27$, $P<0.001$) and protraction lengths ($F_{2,10}=5.94$, $P=0.02$) than hounds and retrievers (Table 2). In contrast, the duration of the forelimb galloping swing phase was significantly longer for retrievers than for northern breeds ($t_{10}=2.23$, $P<0.01$; Table 2).

Energetics

Because body mass differences between groups can bias mass-specific comparisons of oxygen consumption (Packard and Boardman, 1999), we first tested for a possible effect of mass. We used ANCOVA with resting oxygen consumption as the dependent variable, breed group as the main factor and body mass as a covariate. The general linear model was highly significant (GLM: $F_{5,183}=8.2$, $P<0.01$), but body mass was not a significant covariate (mass: d.f.=1, $F=2.5$, $P=0.12$), nor was its interaction with breed group significant (breed \times mass interaction: d.f.=2, $F=2.9$, $P=0.08$). We therefore assumed that mass-specific oxygen consumption rates appropriately account for the effect of body mass within the comparatively small mass range of the dogs in our study. We used these rates for all subsequent analyses to compare energy demand of the dogs with data from other studies typically reporting \dot{V}_{O_2} on a mass-specific level.

For all dogs, mass-specific metabolic rate increased linearly as a function of locomotor speed (Fig. 3), as described previously for wild and domesticated canids (e.g. Taylor et al., 1982; Weibel et al., 1983) and the majority of other terrestrial quadruped species (Taylor et al., 1982), according to:

$$\dot{V}_{O_2, \text{northern}} = 7.5 + 6.16 \times \text{speed} \quad (1)$$

$$(r^2 = 0.87, N = 84, P < 0.01),$$

$$\dot{V}_{O_2, \text{hound}} = 10.46 + 8.64 \times \text{speed} \quad (2)$$

$$(r^2 = 0.90, N = 42, P < 0.01),$$

$$\dot{V}_{O_2, \text{retriever}} = 5.72 + 8.74 \times \text{speed} \quad (3)$$

$$(r^2 = 0.89, N = 48, P < 0.01),$$

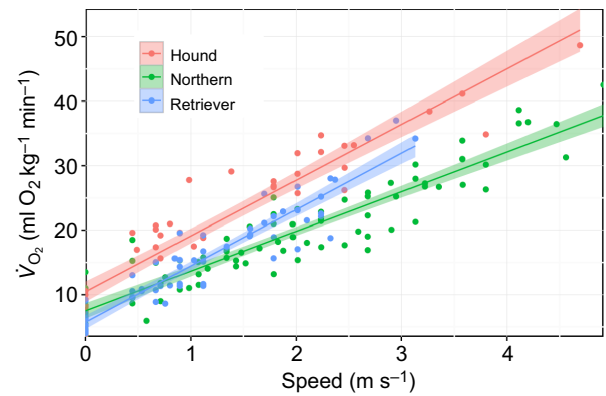


Fig. 3. Mass-specific oxygen consumption plotted as a function of locomotor speed for northern breed, hound and retriever dogs. Each data point is a single \dot{V}_{O_2} trial measurement from a dog moving on the level treadmill at a given speed. Trials were repeated across the full range of speeds for each individual, as determined by prior outdoor running tests. The slopes of the regression lines are net cost of transport (COT_{net}) for each breed and are presented in Eqns 1–3.

where \dot{V}_{O_2} is in $\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ and speed is in m s^{-1} . Hounds had elevated mass-specific \dot{V}_{O_2} across the range of measured trial speeds relative to both northern breeds and retrievers (Fig. 3). Consequently, gait-specific metabolic demands were higher for hounds while walking and trotting ($F_{2,50}=4.7$, $P<0.01$ and $F_{2,83}=16.0$, $P<0.01$, respectively), although galloping energetics did not differ across breeds ($F_{2,5}=1.1$, $P=0.41$). Hounds also exhibited higher and longer mass-specific stride frequencies and lengths, respectively, than retrievers and northern breed dogs during treadmill locomotion.

COT_{tot} ($\text{J kg}^{-1} \text{ m}^{-1}$), which includes locomotor, postural and maintenance costs associated with each animal's RMR (Schmidt-Nielsen, 1972; Williams, 1999), decreased with speed for all individuals within and among dog breed groups (Fig. 4A). Those breeds moving at faster running speeds maximized transport economy. At comparable speeds, northern breeds exhibited lower COT_{tot} than both hounds and retrievers, as indicated by the significantly lower asymptote in our 3-parameter exponential decay model (Table S3). Compared with COT_{tot} of all running mammals (including other canids) presented in Taylor et al. (1982), transport costs for northern breeds were considerably lower than predicted by body mass (Fig. 5). COT_{net} , which includes locomotor demands (including those associated with the posture evoked during locomotion; Halsey, 2016), but not RMR, was also lowest for northern breeds (Fig. 4B; Fig. S1, Table S3). Overall, relative metabolic costs associated with both maintenance and locomotion were lowest for northern breeds as mass-specific resting costs were similar (approximately 6 – $8 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) across breed groups; Fig. S1).

Faster speeds significantly reduced the mass-specific energy cost per stride ($\text{J kg}^{-1} \text{ stride}^{-1}$) for hounds (cost per stride = $-0.299 \times \text{speed} + 5.49$, $r^2=0.14$, $N=29$, $P=0.05$) but not retrievers ($P=0.11$) or northern breed dogs ($P=0.7$). Across all speeds, the mean metabolic cost per stride was significantly lower for northern breeds ($3.47 \pm 0.09 \text{ J kg}^{-1} \text{ stride}^{-1}$) than retrievers ($3.84 \pm 0.12 \text{ J kg}^{-1} \text{ stride}^{-1}$) and hounds ($5.00 \pm 0.15 \text{ J kg}^{-1} \text{ stride}^{-1}$; $P=0.05$ and $P<0.01$, respectively; Fig. 4C). Indeed, energetic demands associated with trotting in northern breeds were significantly lower than those of walking and galloping ($F_{2,67}=6.7$, $P<0.01$; Fig. 4), indicating the metabolic economy of

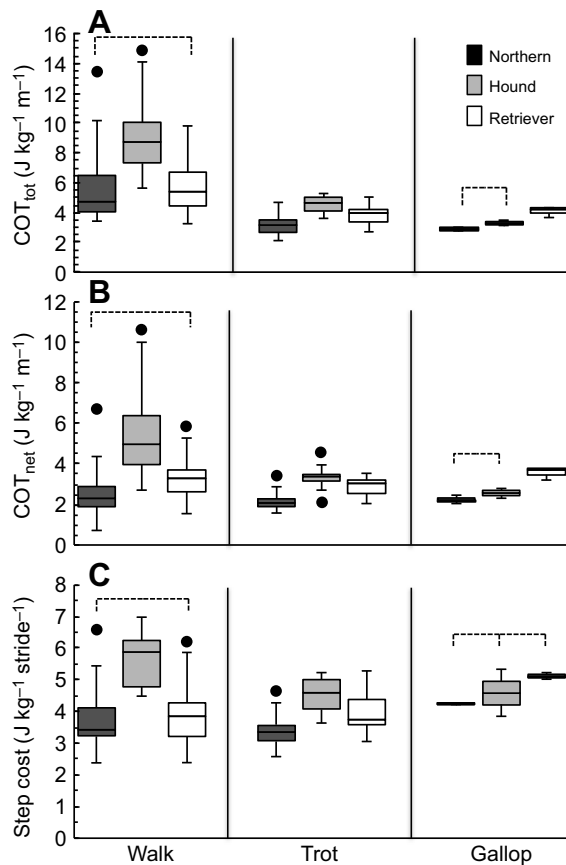


Fig. 4. Mass-specific energetic costs associated with the cost of transport and cost per stride. (A) Total cost of transport (COT_{tot}), (B) COT_{net} and (C) cost per stride for running dogs. Three locomotor gaits for northern breeds, hounds and retrievers were compared. Boxes not connected by a dashed line differ significantly ($P < 0.05$). Total COT was lowest while galloping for all groups, and northern breeds had significantly lower COT_{net} and step costs than hounds and retrievers, particularly while trotting.

trotting relative to both slower and faster gaits in this group. Forelimb and hindlimb foot contact times (t_c) were positively related to these costs per stride in hounds (cost per stride = $3.13 + 4.64t_c$, $r^2 = 0.84$, $P < 0.01$; cost per stride = $3.17 + 4.5t_c$, $r^2 = 0.89$, $P < 0.01$, respectively), but had no effect on retriever and northern breed dogs ($P = 0.67$ – 0.82 range).

DISCUSSION

Although dogs in general possess a suite of adaptations for aerobic locomotion (reviewed in Taylor et al., 1987b), the between-group differences we observed in the present study reflect a physiological signature of artificial selection in the economy of running by different dog breeds. We found that this was manifested as breed-specific differences in both overground stride mechanics and treadmill-derived movement energetics among northern breed, hound and retriever groups. Thus, faster speeds promoted maximum economy for all dogs, but northern breeds had the lowest COT_{tot} , COT_{net} and cost per stride levels relative to hounds and retrievers when trotting and galloping (Fig. 4).

Our hypothesis, that dog breeds more closely related to their gray wolf progenitor have relatively lower COT, was empirically supported (Fig. 4; Fig. S1, Table S3). Hounds and retrievers are both relatively modern breeds compared with the ancient lineage that includes northern breed dogs (Huson et al., 2010; Parker et al.,

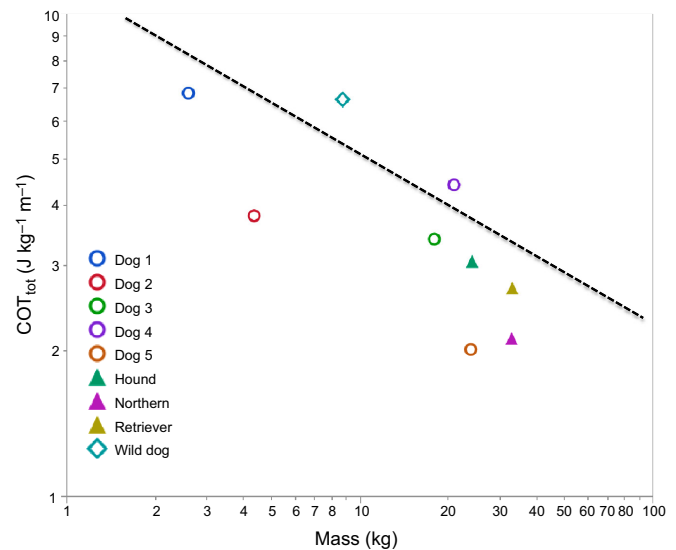


Fig. 5. COT_{tot} for various canids in relation to the allometric regression of Taylor et al. (1982) for running mammals: $COT_{tot} = 10.7 \times \text{mass}^{-0.32}$ (dashed line). Filled triangles are data from the present study; open symbols represent data from dogs (breeds not specified) and African wild dogs running on a level treadmill as presented in Taylor et al. (1982). All dogs measured in the present study had lower transport costs than predicted by body mass, and this was particularly true for the northern breed dogs.

2004; Vonholdt et al., 2010; Wang et al., 2013). Genetically, the ancient breeds cluster together closest to gray wolves, but the group is surprisingly diverse in morphology and origin. This group includes the akita and chow chow of Asian origin, the saluki and Afghan hounds from the Middle East, the African basenji, and the northern breeds we assessed (Parker, 2012). Our study suggests that over the last $\geq 15,000$ years of domestication, selective breeding has altered the aerobic locomotor economy of dogs, with the northern breeds retaining an economical physiological foundation that originated with gray wolves. To date, the limited existing data on the metabolic cost of running in wolves (Taylor et al., 1982; Weibel et al., 1983) does not indicate superior locomotor energy economy in wolves. However, comparisons with the current study may be misleading as a result of the adult ages of our dogs and the immature age of the wolves in the previous studies. Consequently, additional studies that measure ecologically relevant metabolic rates of adult wolves at endurance speeds are needed to determine the similarities or differences in locomotor energetics of wolves and domesticated dogs of comparable morphology and age.

To determine whether interbreed differences in energetic costs per stride were related to variation in gait patterns, we compared the Froude numbers for each breed at the walk–trot and trot–gallop transition speeds. Previous work has shown that animals of different masses but moving at the same Froude number are dynamically similar, and hence use the same gait, have comparable foot phase relationships, relative stride lengths and duty factors, and exert similar ground reaction forces (Alexander, 1984, 2005; Alexander and Jayes, 1983). At the walk–trot gait transition, our results reflected those of prior studies (e.g. Jayes and Alexander, 1978; Maes et al., 2008) where dogs began trotting at Froude numbers ≤ 0.5 . However, dogs in our study began galloping at Froude numbers around 1 (mean = 0.93 ± 0.07), much lower than the predicted Froude numbers (≥ 3) reported in the previous studies. Both lower sample sizes and space constraints of the previous studies (Jayes and Alexander, 1978; Maes et al., 2008) may have

contributed to these differences in Froude numbers when comparing our trials of 23 individual dogs running off-leash along an outdoor course.

When compared with the gait mechanics predictions of Heglund and Taylor (1988), we found that hounds and retrievers, but not northern breeds, trotted and transitioned from trot to gallop at speeds significantly faster than expected based on body mass (Fig. 2). The original study by Heglund and Taylor (1988) developed allometric equations concerning the effects of body size on stride mechanics from 16 species of wild and domestic quadrupeds ranging in mass from 30 g mice to 680 kg horses. Domestic dogs represented the only carnivore species in their analysis. It is noteworthy that in the present study, the two breed groups that differed significantly from the predicted mechanics, the hounds and retrievers, also showed significantly higher mass-specific COT and stride costs for these gaits than northern breed dogs (Fig. 4). In contrast, the stride mechanics of the northern breeds were as predicted. Overall, centuries of selective breeding for hunting performance in hounds and retrievers may have increased the preferred speed range for these breeds (Fig. 1; Table S2), with ensuing reduced locomotor economy (Fig. 4; Table S3).

Despite differences in basic stride mechanics across breeds, detailed kinematic analyses revealed limited distinctions between groups. Based on 24 kinematic parameters, we found larger forelimb retraction lengths and angles while trotting for hounds compared with northern breeds and retrievers (Table 2). This wider forelimb swing resulted in longer stride lengths and faster stride frequencies for hounds, which may have contributed to their higher COT and stride costs while trotting (Fig. 4). In contrast, northern breeds were the only group in which the mass-specific stride costs associated with trotting were significantly lower than those of both walking and galloping (Fig. 4C), resulting in relative energy economy for this intermediate-speed gait. This group also exhibited reduced vertical displacement while trotting compared with walking (Table 2). Such ‘spring dampening’ while loading the Achilles tendon at speed reduces damaging vibrations and enhances forward propulsion with subsequent energy savings (Alexander, 2001; Hermanson, 1997; Reilly et al., 2007; Wilson et al., 2000, 2001), which is consistent with our metabolic measurements (Fig. 3).

More generally, most terrestrial quadrupeds exhibit two unique mechanisms for reducing muscular work, and hence energy expenditure, during locomotion: pendular and mass-spring dynamics (Biewener, 2006; Cavagna and Kaneko, 1977; Cavagna et al., 1977; Hoyt et al., 2006). At walking speeds, animals exchange kinetic energy with potential energy of their center of mass (CoM) through an inverted pendulum mechanism (Cavagna et al., 1977; Griffin et al., 2004). Pendular energy savings persist even for loaded and incline locomotion (Gomeñuka et al., 2014; Pontzer, 2016), although the benefits of this mechanism diminish at faster speeds (Gomeñuka et al., 2016). For running gaits, a spring–mass mechanism predominates, where stretched elastic structures (ligaments and tendons) store and recover mechanical energy (Alexander, 1988; Blickhan, 1989; Cavagna et al., 1977, 1988). In the present study, the economical trotting gait of northern breed dogs likely suggests optimized spring–mass energy savings compared with other breeds. This is consistent with observations of these animals during endurance activities and races. For example, Greenland sled dogs are capable of trotting at 2.5 m s^{-1} for 8–10 h each day for 2–3 days, covering 60–80 km daily (Gerth et al., 2010). Similarly, wolves routinely travel in the trotting gait at the same speed (2.4 m s^{-1} ; Mech, 1994) and can cover 76 km in 12 h (Mech and Cluff, 2011).

Foot t_c , described as the stride’s stance phase duration, decreases as a power function of speed (Hoyt et al., 2000) and has been shown to be inversely related to the energy expended per stride (Alexander and Ker, 1990; Kram and Taylor, 1990). Regardless of differences in the COT, we found no significant difference in hindlimb kinematics, including t_c , across gaits for the three dog breed groups (Table 2). Rather than limb kinematics per se, body posture and its relationship to kinematics may play a role in the COT of these groups. To examine this proximate mechanism, we digitally measured hip angle while standing (top of scapula to hock; Table S1) from lateral-view photographs of the study animals and American Kennel Club breed standards (www.akc.org/dog-breeds/), as well as gray wolves. Northern breeds exhibited a more upright stance, with the hindlimbs positioned closer to their CoM (mean hip angle= 109.4 ± 1.1 deg; Fig. 6B), nearly identical to that of gray wolves (mean hip angle= 108.8 ± 1.7 deg, $F_{3,31}=33.7$, $P=0.99$; Fig. 6A). In contrast, the hindlimbs of both hounds and retrievers were distally grounded, farther from their CoM with significantly wider hip angles than observed in northern breeds (mean hip angle= 121.4 ± 1.7 and 122.2 ± 1.2 deg, respectively; $F_{2,27}=38.6$, $P<0.01$ for both; Fig. 6C,D). Hounds and retrievers also held their heads in more upright positions while running, relative to the comparatively flat toplines of wolves and northern breed dogs (Fig. 6E–H).

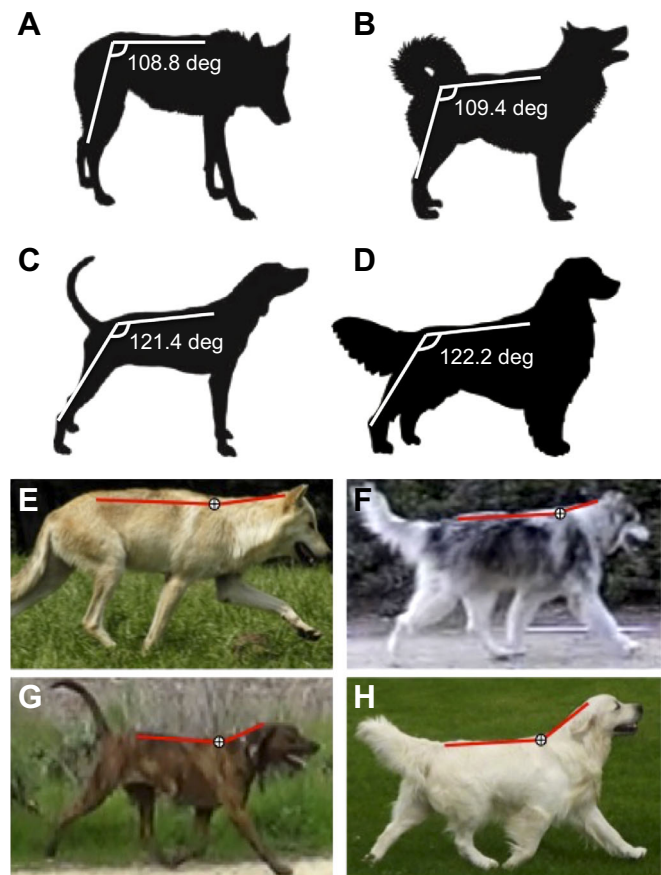


Fig. 6. Comparative hip and topline angles of gray wolves and study dogs. (A,E) Gray wolves ($N=5$), (B,F) northern breed dogs represented by an Alaskan malamute ($N=15$), (C,G) hounds ($N=5$) and (D,H) retrievers ($N=10$). Hip angles (A–D) were approximated from the top of the scapula to the hip’s iliac crest to the hindlimb hock. Canid outlines from www.clipartof.com. Topline angles (E–H) are approximated as the obtuse angle from the flat of the back to the back of the head, with hounds and retrievers running with their heads in more upright positions than observed in wolves or northern breed dogs.

Although this is a preliminary assessment, there are several mechanical advantages of the upright stance and flat topline of northern breed dogs and wolves that could impact the energetic costs of running. By aligning the joints and segments of the hindlimbs more closely with the ground reaction force vector exerted at the foot (Gray, 1968), the more proximal and erect orientation of northern breed hindlimbs reduces excessive bone and muscle stress (Biewener, 1989). It also provides an effective mechanical advantage for loading the tendons of the leg muscles and ligaments of the foot (Alexander and Ker, 1990; Biewener, 1989, 1998; Reilly et al., 2007), likely contributing to the relative locomotor economy observed in northern breeds. These connective tissues function like ‘springy struts’ (Wentink, 1979) or pogo sticks to temporarily store, then return, the elastic strain energy necessary to move the limb and body (reviewed in Alexander, 1990, 2002; Blickhan, 1989; Ker, 1981; Taylor, 1994) and are especially important during trotting (Cavagna et al., 1977; Gregersen et al., 1998).

Several studies have investigated the muscle–tendon architecture of the canid hindlimb (Shahar and Milgram, 2001) and its effect on speed and power generation (Kemp et al., 2005; Pasi and Carrier, 2003; Williams et al., 2008), but the role of comparative functional anatomy in promoting locomotor economy across dog breeds and canids in general remains largely unexplored. Here, we speculate that specialized tendon loading and energy recovery may provide a natural mechanism enabling wolves and other large canids to track prey over long distances (e.g. Mech et al., 2015; Sheldon, 1992). When retained through domestication, such a mechanism may help explain the exceptional physiological performance of northern breed dogs during extreme distance events such as the 1600 km Iditarod Trail race and other endurance trials (Gerth et al., 2010; Hinchcliff et al., 1997; Miller et al., 2014; Van Citters and Franklin, 1969).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

C.M.B. and T.M.W. conceived and designed the study. C.M.B. and T.M.W. conducted all experiments. C.M.B. analyzed the data and wrote the manuscript with editorial advice provided by T.M.W.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.144188.supplemental>

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