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The musculoskeletal anatomy of the reindeer (*Rangifer tarandus*): fore- and hindlimb

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Abstract Reindeer are numerous and widespread across the northern Holarctic. They are efficient long distance migrants and are able to cope with variations in substrate, such as ice, snow, uneven forest floor, wetland and flat grassland. However, as with the vast majority of quadrupedal vertebrates, no quantitative musculoskeletal anatomical information exists for these animals making it difficult to analyse the biomechanics of their locomotor behaviour. In this paper, we describe the gross anatomy of the limb musculature and quantify muscle and tendon morphology. Reindeer show slight hindlimb dominance in muscle and tendon mass, with muscle mass primarily proximally situated and tendon distally situated. Extensor muscles are heavier than flexors, but tendon mass is broadly similar in both extensors and flexors. The only complete quadrupedal data sets available for comparison are for hares and greyhounds making it difficult to identify general patterns. There are no obvious body mass effects and reindeer often comes out as intermediate between hare and greyhound. However, greyhound seem less hindlimb dominated in terms of muscle but both greyhound and hare have much higher masses of tendon compared to reindeer, particularly in their hindlimbs. All these quadrupeds show the commonly observed trait of much larger tendons and less massive muscles in distal limb segments; this reduces the inertial cost of accelerating the limbs. Generally, there is a dearth of available quantitative anatomical data of complete animals. This lack of information is hindering attempts to gain a better understanding of musculoskeletal function in quadrupeds.

Keywords Myology · Muscle · Tendon · Locomotion

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Introduction

Reindeer belong to the Cervidae family of the order Artiodactyla. The evolutionary history of reindeer is still under debate, with several theories being presented (Rankama and Ukkonen 2001; Flagstad and Røed 2003; Ukkonen et al. 2006). Radiocarbon dating has placed reindeer populations as far back as the late Pleistocene (Lie 1986; Guthrie 1990), with their current distribution pattern, in the northern hemisphere, thought to be due to migration affected by glacial periods and their ability to adapt to extreme weather conditions. Most reindeer are known to migrate long distances between seasons in accordance with food distribution (Skogland 1980; Mårell et al. 2002; Ferguson and Elkie 2003). However, due to specific habitats, some are noted to undertake only small migrations, such as, the semi-domesticated populations of Eurasian mountain reindeer (*R. t. tarandus*) in Troms county, Norway (Weladji and Holand 2006) and the Svalbard reindeer (*R. t. platyrhynchus*; Tyler and Oritsland 1989). Reindeer are also known to migrate short distances within the summer season in response to insect harassment (Skogland 1984; Skarin et al. 2004; Vistnes et al. 2008).

Reindeer migrate seasonally over long distances on land and as such possess a range of anatomical adaptations typical of cursorial animals (for review see Preuschoft et al. 1994). However, in some reindeer populations (caribous), these migrations cover greater distances than in any other terrestrial mammal (Fancy et al. 1989) and it would be reasonable to assume that their anatomy differs from that of other ungulates. One area where specialisation is seen is in specific adaptations of foot morphology for use on different substrates (Köhler 1993). For example, *Rangifer* possess well-developed and relatively large dewclaws. These are generally reduced or absent in other ungulates, and their function is uncertain since they rarely touch the ground except in unusual substrate conditions (Telfer and Kelsall 1984; Gough-Palmer et al. 2008). In reindeer, the dewclaws reach the ground and provide a larger foot surface area which, when compared with other mammals, results in a greater locomotive ability on snow and, therefore, may have a direct influence on this species' ability to avoid predation (Telfer and Kelsall 1984; Kojola et al. 2004). In addition, reindeer demonstrate a high oxidative capacity of all fibres in their skeletal muscle, which may be linked to endurance activity (Essén-Gustavsson and Rehbinder 1985), although in the Svalbard reindeer subspecies, the large content of αW fibres has been linked to the use of muscle protein for nutritional purposes (Kiessling and Kiessling 1984). However, there are few quantitative studies on the morphology of the muscles and associated tendons in these animals, despite the fact that this is a popular research area especially for primates [e.g. howler monkeys (Grand 1968), great apes and humans (Payne et al. 2006; gibbons Michilsens et al. 2009)]. There is some quantitative data available on muscle and bone masses from the meat production industry (Wiklund et al. 2008), but these studies lack the anatomical specificity to be useful in detailed scientific studies. Good comparative data exist for hare (Williams et al. 2007a, b) and greyhound (Williams et al. 2008a, b), but the extensive data available for horses are incomplete and comes from widely varying individuals, which therefore makes it difficult to produce a consistent single comparative data set (e.g. Brown et al. 2003; Payne et al. 2005a, b). In general, there is a lack of consistency and completeness in data collection in many studies: often only a single limb or part of a limb is presented and basic key information such as tendon mass may be completely missing.

The aim of this study was to examine the quantitative functional gross anatomy of the complete locomotive musculature and associated tendons in the reindeer. This information is essential for both detailed musculoskeletal modelling and comparative biomechanical analysis of the musculoskeletal system.

Materials and methods

Two thoracic and two pelvic limbs, from a 13-month-old male Eurasian mountain reindeer (*Rangifer tarandus tarandus*) weighing 91 kg, were used in this study. The reindeer was obtained from a semi-domesticated herd belonging to Sámi pastoralists. It was killed for an unrelated study, and the specimen was eviscerated and its head removed and stored at −20°C until required for dissection. The limbs and torso were skinned, and the muscles and associated tendons were dissected, identified and described. Careful attention was paid to the origins and insertions of these muscles, as it was expected that they would differ to some degree from other ungulates. The muscles and tendons were then removed, and the total length and belly length, where appropriate, of each muscle was recorded using a ruler. Muscle length was measured and defined as the distance between the proximal and distal fibres. External tendons were removed where present and their length measured using the same method. The masses of individual muscles, muscle bellies and tendons were recorded to the nearest gram using digital scales. Five fibre length samples were taken from each muscle or muscle belly at random points using a ruler, and an average fibre length was calculated. A resting pennation angle of the non-extended limb, where appropriate, was also recorded by measuring the angle between the internal or external tendon and the direction of the muscle fibres using a protractor. Five pennation angles were recorded from different areas of the muscle, and an average was calculated.

Using the recorded data, muscle physiological cross-sectional area (PCSA) was calculated by dividing muscle mass by muscle density (1,060 kg m^{-3}, Mendez and Keys 1960; Brown et al. 2003) to give muscle volume, and dividing this by the mean fibre length. Tendon cross-sectional area (CSA) was similarly calculated by dividing tendon mass by tendon density (1,100 kg m^{-3}, Watson and Wilson 2007) to give tendon volume, and dividing this by tendon length.

Results

The attachment areas of the muscles investigated in the forelimb are shown in the Online Resource 3 and illustrated in Figs. 1, 2, 3, 4, 5. Online Resource 4 shows the attachment areas of the muscles investigated in the hindlimb. These are illustrated in Figs. 6, 7, 8. M. brachioradialis, m. pronator teres and m. pectineus could not be identified on the specimens available. These muscles may be either absent or greatly reduced in reindeer.

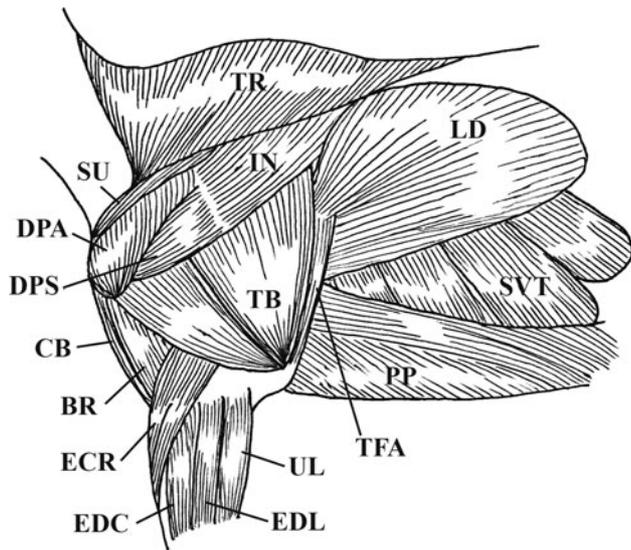The Online Resources 5 and 6 show the muscle and tendon dimensions recorded for the forelimb and hindlimb,

Fig. 1 The superficial muscles of the shoulder as visible after the removal of the skin and overlying fascia (lateral view). *TR m.* trapezius, *IN m.* infraspinatus, *LD m.* latissumus dorsi, *SU m.* supraspinatus, *DPA m.* deltoideus pars scapularis, *DPS m.* deltoideus pars acromialis, *TB m.* triceps brachii accessory head/lateral head, *SVT m.* serratus ventralis (thoracic part), *PP m.* pectoralis profundus, *CB m.* cleidobrachialis, *BR m.* brachialis, *ECR m.* extensor carpi radialis caudal head, *ECR m.* extensor carpi radialis caudal head, *EDC m.* extensor digitorum communis, *EDL m.* extensor digitorum lateralis, *UL m.* ulnaris lateralis and *TFA m.* tensor fasciae antebrachii
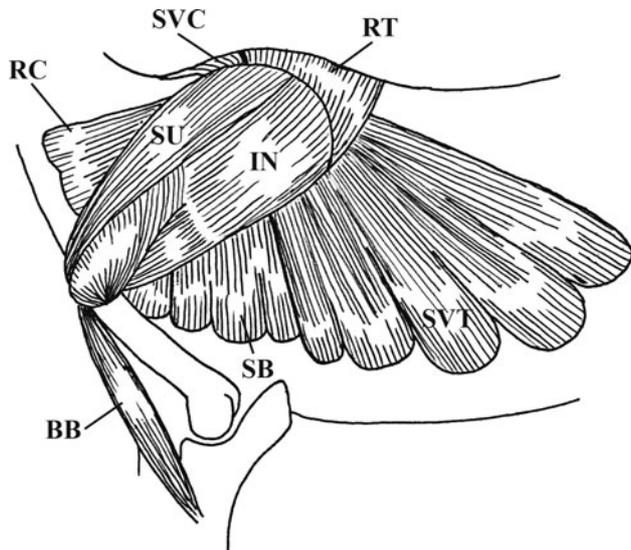

Fig. 3 The deep muscles of the shoulder and the superficial muscles of the elbow region (lateral view). *TMA m.* teres major, *TMI m.* teres minor, *TB m.* triceps brachii lateral head, *BR m.* brachialis, *CB m.* cleidobrachialis, *BB m.* biceps brachii, *ECR m.* extensor carpi radialis caudal head, *EDC m.* extensor digitorum communis, *EDL m.* extensor digitorum lateralis and *UL m.* ulnaris lateralis

Fig. 2 The deep muscles of the shoulder as visible after the removal of the superficial muscle layer (lateral view). *RC m.* rhomboideus cervicis, *SVC m.* serratus ventralis (cervical part), *RT m.* rhomboideus thoracis, *SU m.* supraspinatus, *IN m.* infraspinatus, *SB m.* subclavius, *SVT m.* serratus ventralis (thoracic part) and *BB m.* biceps brachii

Fig. 4 The deep muscles of the elbow region (lateral view). *FDU m.* flexor digitorum profundus ulnar portion, *FCR m.* flexor carpi radialis, *FCU m.* flexor carpi ulnaris, *FDS m.* flexor digitorum superficialis and *FDH m.* flexor digitorum profundus humeral portion deep head

respectively. These data are the means of the left and right limbs. To investigate locomotor function, it is useful to aggregate the information into functional groups. Unfortunately, many muscles do not have a simple function: complexities include muscles t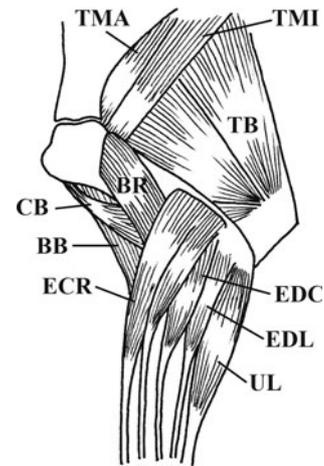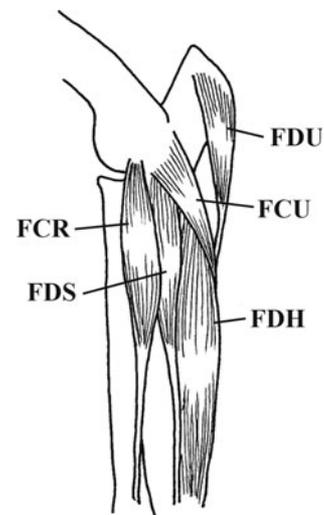hat act across multiple joints and muscles whose moment arm changes with joint excursion so that their action changes completely. Online Resources 7 and 8 detail how we have attempted to group muscle function. Muscles were assigned a function about each joint based on the standard textbook description of each muscle (Skerritt 1984), and in the absence of moment arm data, if a muscle affected a torque over multiple joints, then its contribution was subdivided equally among these joints. This allows the calculation of muscle contribution by joint and also simple functional classification. This information has been summarised (Online Resource 1). Mass and cross-sectional area
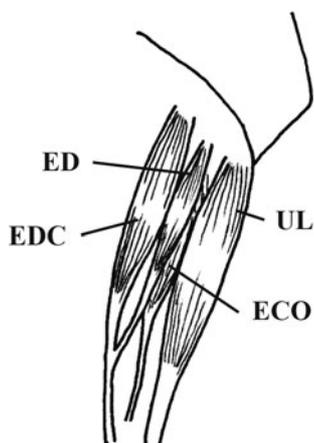
Fig. 5 The deep muscles of the elbow region (medial view). *ED m.* extensor digiti II, *UL m.* ulnaris lateralis, *EDC m.* extensor digitorum communis and *ECO m.* extensor digitopum lateralis
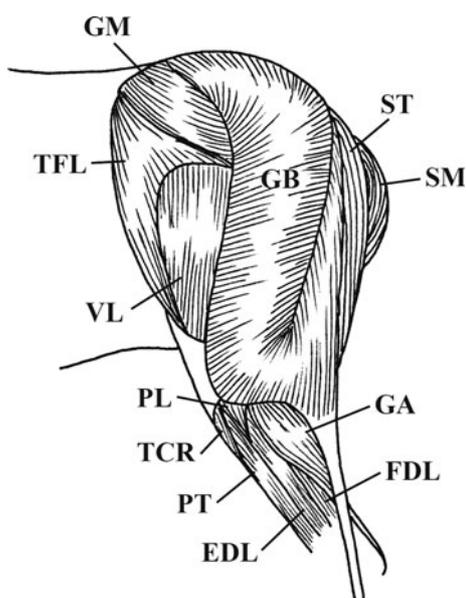

Fig. 7 The deeper muscles of the hip and knee as visible after the removal of the superficial muscle layer (lateral view). *GP m.* gluteus medius cranial head, *GE m.* gemelli, *AL m.* adductor longus, *VL m.* vastus lateralis, *TFL m.* tensor fasciae latae caudal head, *ST m.* semitendinosus, *SM m.* semimembranosus, *GA m.* gastrocnemius, *PL m.* peroneus longus, *TCR m.* tibialis cranialis, *PT m.* peroneus tertius, *FDS m.* flexor digitorum longus and *EDL m.* extensor digitorum lateralis

Fig. 6 The superficial muscles of the hip and knee as visible after the removal of the skin and overlying fascia (lateral view). *GM m.* gluteus medius, *ST m.* semitendinosus, *GB m.* gluteobiceps, *SM m.* semimembranosus, *TFL m.* tensor fasciae latae caudal head, *VL m.* vastus lateralis, *PL m.* peroneus longus, *GA m.* gastrocnemius, *TCR m.* tibialis cranialis, *PT m.* peroneus tertius, *FDL m.* flexor digitorum longus and *EDL m.* extensor digitorum lateralis

Fig. 8 Deep muscles around the hip (lateral view). *VM m.* vastus medialis, *SA m.* sartorius cranial part, *GR m.* gracillis and *SM m.* semimembranosus

values are simply summed using the multiple joint factors as appropriate to give the total contribution. The fibre and tendon length values are the mean values obtained by dividing total volume by total cross-section.

When considering muscle mass, 58% is found in the hindlimb and 42% in the forelimb; 56% acts over the proximal joints (shoulder and hip), 31% over the intermediate joints (stifle and elbow) and 13% over all the more distal joints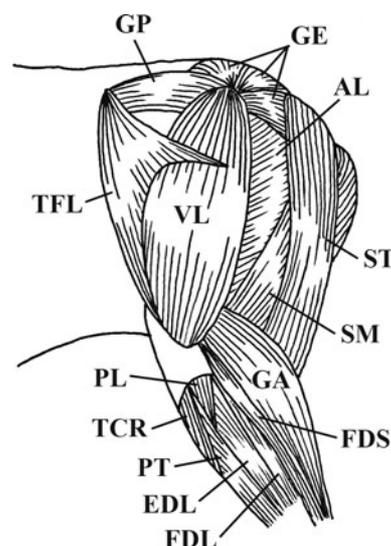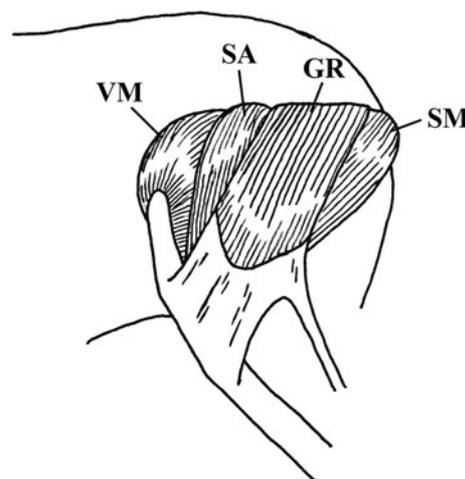 (tarsal, carpal and digital joint); 59% can be described as extensor and 30% as flexor, and 11% has another action. The pattern of fibre length variation in these groupings is very similar to the pattern of muscle mass variation: the correlation coefficient between fibre length and muscle mass is 0.90; the coefficient of variation of muscle mass is 0.4 and of fibre length is 0.33. In contrast, the muscle physiological cross-sectional area is remarkably evenly distributed among the different compartments: correlation coefficient between PCSA and muscle mass is 0.72; coefficient of variation of PCSA is 0.19. This suggests that

muscle force requirements are similar at proximal, intermediate and distal joints and also between extensors and flexors, whereas the power requirements are concentrated proximally and in the extensors.

When considering tendon mass, 62% is found in the hindlimb and 38% in the forelimb; 18% acts over the proximal joints (shoulder and hip), 32% over the intermediate joints (stifle and elbow) and 50% over all the more distal joints (tarsal, carpal and digital joint); 46% can be described as extensor and 50% as flexor, and 4% is associated with another action. The pattern of tendon length variation in these groupings is again very much the same as the mass distribution although the relationship is not as close as for muscle: the correlation coefficient between tendon length and tendon mass is 0.70; the coefficient of variation of tendon mass is 0.32 and of tendon length is 0.41. Tendon cross-sectional area shows much less variation: correlation coefficient between tendon CSA and tendon mass is 0.29; coefficient of variation of tendon CSA is 0.21. This supports the idea that the force requirements are similar, but the energy storage is concentrated distally and in the hindlimbs.

When comparing muscle data, there are a large number of possible comparisons. However, because mass, length and cross-sectional area are all highly correlated and because the available data are relatively small, it was decided to concentrate on mass. This parameter was chosen because it is the easiest value to measure accurately, and, as explained in the 'Introduction', its mechanical interpretation is largely independent of moment arm information, which we were unfortunately unable to obtain. Online Resource 2 shows how the reindeer results compare with two other quadrupedal species. Unfortunately, the only good comparative data sets that currently exist are limited to hare (Williams et al. 2007a, b) and greyhound (Williams et al. 2008a, b), and these summary values are shown in the figure. For reindeer, forelimb muscles (summed for both limbs) make-up 10.9% of total body mass and hindlimb muscles 14.8%. This is broadly similar to the hare (10.5 and 16.7%), but the forelimb muscle mass in the greyhound is appreciably higher (18.3%) although the hindlimb mass is similar 17.1%. The pattern of distribution of this mass around the joints is similar in all three species with most of the muscles acting proximally (reindeer 14.5, 7.9, 3.3%; hare 16.9, 7.7, 2.5%; and greyhound 22.7, 10.2, 2.5%). Again, most of this mass is found in the extensors with appreciably less in the flexors in all three species (reindeer 15.3, 7.7%; hare 12.9, 9.7%; and greyhound 18.9, 12.5%). The differences in tendon mass are much more extreme than the differences in muscle mass. Reindeer have much less tendon mass than either the hare or greyhound although as with the muscle, the pattern of distribution is the same. Thus, in the hindlimb, for example, reindeer have less than

a tenth of the tendon compared with greyhounds (reindeer 0.27, 0.41%; hare 0.74, 2.69%; and greyhound 1.27, 4.25%). This difference is only slightly less extreme when looking at the other divisions (Joints: reindeer 0.12, 0.22, 0.35%; hare 0.47, 0.70, 2.27%; and greyhound 0.75, 1.81, 2.96%. Extensors/Flexors: reindeer; 0.31, 0.35%; hare 1.59, 1.84%; and greyhound 2.65, 2.87%).

Discussion

The descriptions of muscle gross anatomy and function are similar to those classically given for cows and sheep. The conspicuous lack of comparable studies (i.e. in free-ranging quadrupeds of similar size) makes it difficult to relate our findings to locomotor traits that are typical of the reindeer. Our findings should be viewed in the perspective of an ungulate adapted to undertake large migrations on a variety of surfaces; on rocks and wetland tundra and on snow and ice. It is likely that the missing muscles that have been highlighted in the descriptions may simply be reduced in reindeer rather than completely absent. It is important to stress that the data presented here are from a single individual; there is always the possibility of anatomical variation, and a degree of caution is necessary in interpreting the results.

Unfortunately, we were not able to measure reindeer moment arms. Muscle and tendon masses are probably the best indicators of function in the absence of moment arm data. Muscle force is linked to physiological cross-sectional area (PCSA), and rate of contraction is linked to fibre length but to evaluate these functions in the context of locomotion, one must calculate the joint torque and angular velocity, both of which involves multiplication by moment arm. Without the moment arms information, neither of the cross-section or length parameters can be objectively assessed in terms of mechanical function, but they can still be analysed statistically. For a complete picture, it would also be necessary to know the contraction velocity and whilst this can be inferred from fibre type information, this is not available for all the limb muscles. The power output of a muscle, as reviewed by Hill (1950), is directly proportional to its mass irrespective of the moment arm and is therefore a very useful mechanical parameter. Tendon mass is less commonly reported but since the maximum energy storage per gait cycle of a tendon is a function of its mass; it is likely that these values directly relate to the functional importance of the structure again independent of moment arms. This has been shown to be important in horse trotting (Witte et al. 1995). Masses can also be expressed as a percentage of total body mass to allow straightforward cross-species comparison, but there are caveats to this approach. Whilst tendon and muscle mass provide maximum limits to

performance, it may actually be rare that these structures are used maximally. Tendon in particular is often thicker than would be predicted by elastic energy storage alone (Ker et al. 1988), and in humans, the extreme length of some tendons is more likely a result of force control requirements than energy saving (Rack and Ross 1984).

There are no specific data on reindeer in the literature, but we would expect the centre of mass to be somewhat closer to the forelimb and therefore the ground reaction forces to be higher for the forelimb than for the hindlimb, as is typical in most cursorial quadrupeds with the exception of primates (Kimura et al. 1979; Demes et al. 1994; Franz et al. 2005). However, whilst vertical forces are higher in the forelimb, horizontal forces are higher in the hindlimb (as discussed in Payne et al. 2005b), and this may help to explain why the muscle proportion in the hindlimb is higher than in the forelimb. In the absence of moment arm data, forces alone do not justify large muscles since large forces can be achieved in small muscles by having large numbers of very short fibres. The work done by vertebrate muscle per gait cycle is limited to approximately 25 Jkg^{-1} (Askew et al. 2001), which suggests that if the work per gait cycle is higher in the hindlimb than the forelimb then this would justify the additional muscle. The reduction in muscle in distal limb segments is a widespread phenomenon in legged animals and has several advantages. It reduces the moment of inertia by moving mass closer to the pivot point and hence the work required to move the limb (Hildebrand 1995). Moreover, the combination of reduction in moment of inertia and the movement of the centre of mass closer to the pivot point increases the natural pendular frequency of the limb that allows higher speeds without energy input (Witte et al. 1991; Preuschoft et al. 1994). The concentration of muscle in the extensors is again widely found and is almost certainly due to the major requirement of the musculoskeletal system being to act against gravity since work against gravity is probably the largest component to the cost of locomotion (Kram and Taylor 1990). It is not very profitable to comment on fibre lengths and PCSA values in the absence of moment arm data since any functional interpretation depends on the action of muscles around joints and both pieces of information are required. As an aside, it should be noted that the converse is also true: moment arm data without either fibre length or PCSA has very limited interpretational value. However, the pattern of reduced fibre length in distal tendons is striking, and in situations where moment arm data are available, it has been shown in camels (Alexander et al. 1982) and horses (Wilson et al. 2001) that some distal muscles cannot contract far enough to influence the observed angular movements in the distal joints. Whether this is also true in reindeer cannot currently be answered. Comparing across species, the musculature appears to be reasonably consistent given the very different body shapes of the animals available for comparison. The greyhound does have appreciable extra muscle particularly in the forelimb reflecting the high speed locomotor capabilities of this animal.

The patterns of tendon masses are very informative. Tendon acts as a simple damped spring during locomotion and the amount of energy that can be stored, as in any material, depends on the mass. The strain energy storage of tendon is 2,500 Jkg^{-1} at 8% strain (Vogel 2003), and this is therefore the limit of the amount of energy storage available per gait cycle. The ratio of tendon to muscle around the proximal joints in the reindeer is 0.8%, so muscle clearly dominates as the main source of energy there. However, distally, the ratio increases to 2.8 and 10.4% so that it is likely that the main energy source around the distal joints is elastic strain energy stored in the tendons. Tendon is similarly concentrated in the flexors (4.5%) compared with the extensors (2.0%) suggesting that elastic mechanisms may be more important during the swing phase than during the support phase similar to the situation found in horses (Wilson and Watson 2003). What is particularly striking is that unlike the musculature where the differences between species are relatively small, for tendon, there are enormous differences. The importance of tendons as elastic energy stores has been suggested since the 1960s (Cavagna et al. 1964) and demonstrated in a wide range of experiments using both indirect (e.g. Cavagna et al. 1977) and direct measures (e.g. Biewener et al. 1998). It has also been shown that the power requirement in many locomotor performances is too high for muscles alone to generate (e.g. Aerts 1998; Johnson and Buckley 2001), and virtual ablation experiments (Sellers et al. 2010) have isolated the role of tendon in terms of both energy cost reduction and performance gain. Reindeer are particularly noted for their long-distance migration abilities (Nowak 1991), whereas both hares and greyhounds are more likely specialist sprinters (Williams et al. 2007a, b, 2008a, b). This might suggest that the amount of elastic storage needed for an effective 'bouncing ball' gait, and hence, high efficiency is relatively low but that the amount needed for the power amplification necessary for high-speed gait and leaping may be much higher. It is clear that a great deal more comparative data on tendon masses is required before these sorts of questions can be adequately addressed.

Conclusion

The musculoskeletal anatomy of the reindeer follows the standard ungulate pattern qualitatively, and there is currently no comparative data to investigate any quantitative variation within this group. This makes it difficult to assess

the reindeer fore- and hindlimb anatomy to any particular aspects of its life style. For comparison with other quadrupeds, there is still a shortage of data but the basic patterns for muscle mass seem fairly consistent. However, the amount of tendon in reindeer is considerably less than seen in hares and greyhounds but it remains to be seen which of these animals are more typical and what the functional significance of this finding is.

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