Even-toed but uneven in length: the digits of artiodactyls

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Abstract

In captive ruminants housed in small enclosures, characteristic hypertrophy of the outer hooves of the hind limbs is often observed. We hypothesized that the underlying cause is overload attributable to an asymmetry of the digits, especially with respect to their length. To test this hypothesis, the bones of the digits of four species of artiodactyls, which included 11 wild chamois (Rupicapra rupicapra), 11 captive fallow deer (Dama dama), 11 captive bison (Bison bison) and 11 European moose (Alces alces; 9 wild, 2 captive), were radiographed post mortem, and measured using a computer program. In addition, the dimensions of the outer and inner hooves were measured directly with a calliper that had an accuracy of 0.1 mm. The mean lengths of the epiphysis of the fourth metacarpal/metatarsal bone and the first and second phalanges of the fourth digit were greater than that of the third digit, whereas the third phalanx of the third digit had a greater mean length. The fourth digit of the forelimbs was an average of 0.5 mm longer in the chamois, 0.9 mm in the fallow deer, 3.0 in the bison and 2.9 longer in the moose. In the hind limbs, the fourth digit was an average of 3.0 mm longer in the chamois, 1.4 mm in the fallow deer, 2.3 mm in the bison and 5.3 mm in the moose. The mean total length of the fourth digit of the fore limbs was greater than that of the third digit in 73 - 95 % of specimens, depending on species. In the hind limbs, the fourth digit was longer in 91 - 100 % of the specimens. The hooves of the fourth digit were significantly broader than the hooves of the third digit, whereas the inner hooves of the third digits had a greater toe length than those of the fourth digit. The paired digits of artiodactyls are uneven in length, which suggests a different function during stance and weight bearing. It is conceivable that this asymmetry is the result of selection processes that favoured locomotion on soft ground.
Even-toed but uneven in length: the digits of artiodactyls

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Summary

In captive ruminants housed in small enclosures, characteristic hypertrophy of the outer hooves of the hind limbs is often observed. We hypothesized that the underlying cause is overload attributable to an asymmetry of the digits, especially with respect to their length. To test this hypothesis, the bones of the digits of four species of artiodactyls, which included 11 wild chamois (Rupicapra rupicapra), 11 captive fallow deer (Dama dama), 11 captive bison (Bison bison) and 11 European moose (Alces alces; 9 wild, 2 captive), were radiographed post mortem, and measured using a computer program. In addition, the dimensions of the outer and inner hooves were measured directly with a calliper that had an accuracy of 0.1 mm.

The mean lengths of the epiphysis of the fourth metacarpal/metatarsal bone and the first and second phalanges of the fourth digit were greater than that of the third digit, whereas the third phalanx of the third digit had a greater mean length. The fourth digit of the forelimbs was an average of 0.5 mm longer in the chamois, 0.9 mm in the fallow deer, 3.0 in the bison and 2.9 longer in the moose. In the hind limbs, the fourth digit was an average of 3.0 mm longer in the chamois, 1.4 mm in the fallow deer, 2.3 mm in the bison and 5.3 mm in the moose. The mean total length of the fourth digit of the fore limbs was greater than that of the third digit in 73 – 95 % of specimens, depending on species. In the hind limbs, the fourth digit was longer in 91 – 100 % of the specimens. The hooves of the fourth digit were significantly broader than the hooves of the third digit, whereas the inner hooves of the third digits had a greater toe length than those of the fourth digit. The paired digits of artiodactyls are uneven in length, which suggests a different function during stance and weight bearing.
It is conceivable that this asymmetry is the result of selection processes that favoured locomotion on soft ground to provide better traction.
Introduction

Even-toed ungulates (artiodactyls) have an even number of digits (two or four) on each foot. Ruminants, which have two main digits, are the most prominent representatives of the artiodactyls. They have achieved and maintained a worldwide distribution mainly because of their efficient digestive system (Gentry, 1978). Some ruminants, which were domesticated long ago and have been used intensively, are still able to survive in ever-decreasing natural habitats. Wild ruminants such as fallow deer (*Dama dama*) and bison (*Bison bison*) are also farmed, but less commonly than cattle, goats or sheep.

Domestic cattle are often housed on hard surfaces, which leads to the development of characteristic hoof lesions (Sogstad et al., 2005; Somers et al., 2005). In the vast majority of cases the outer hoof increases in size disproportionately with age (Nuss and Paulus, 2006) and is predisposed to sole ulcers or white line disease. Similarly, when wild ruminants are kept in captivity, enlargement and abnormalities of the outer hooves of the hind limbs occur (Fowler, 1980). Although a similar, albeit small, difference in the size of the paired hooves was observed in a wild moose (Kendelbacher, 1935), a difference in hoof size has not been recognized in wild ruminants. It is conceivable that digit characteristics of ruminants are the result of a natural selection process that favoured locomotion on soft ground. This assumption is supported by a preference of domestic cattle for soft flooring and by the observation that diseased hooves recover when cattle have access to pasture (Flower et al., 2007; Hernandez-Mendo et al., 2007).

All ruminants have a metapodium that is composed of the two fused third and fourth metacarpal/metatarsal bones. This composite bone, also called the cannon bone, provides two separate epiphyses for the third and fourth digits (the acropodia), which themselves are composed of the three phalanges. Until recently it was
assumed that the two digits and hooves of artiodactyls are equal in size (Manning et al., 1990) and that the plane of symmetry of each foot passes between the third and fourth digit (Fox and Myers, 2001). However, there are reports of differences in the length and width of the cannon bone epiphyses and the digital bones in cattle (Nacambo et al., 2007; Schwarzmann et al., 2007). Compared with the partner condyle, the condyles of the fourth digit were longer and those of the third digit were wider. These differences were also observed in cattle bones that were several thousand years old (Paral et al., 2004). A recent report described similar differences in the cannon bone and digits of three dromedaries (Camelus dromedarius) (Farhadian and Soroori, 2006). Based on these studies, our hypothesis was that the two digits of ruminants, a suborder of the artiodactyla, are anatomically different, i.e., that the fourth digit is longer and has a larger hoof.

Materials and Methods

To test the hypothesis, the feet of artiodactyls, which included 11 chamois (Rupicapra rupicapra), 11 fallow deer (Dama dama), 11 bison (Bison bison) and 11 moose (Alces alces), were collected immediately post mortem and frozen until further analysis (Keller, 2007). Different wild ruminant species were investigated in order to include different weight classes and habitats (Tab. 1). The chamois were wild and originated from the Swiss Alps. Nine of the moose were wild and originated from their natural habitat in Finland, and two had been kept in small enclosures in a wildlife park in Switzerland. The fallow deer had been kept in a wildlife park with grassland and forest. The bison came from various environments; four originated from large pastures on a farm, six from a wildlife park and one from a zoo. The feet were collected and examined post mortem. Radiographs were taken with a mobile X-ray unit (Gierth HF 200) and type 3A IP digital cassettes (Fuji Systems). The feet were
placed on their dorsal surface and the beam directed palmaro-/plantarodorsally and
centred between the digits at the level of the second interphalangeal joint. The
exposure settings were 70 kV, 25 mA and 0.2 s for the moose and bison feet, and 56
kV, 30 mA and 0.2 s for the chamois and fallow deer feet. The focus-to-film distance
was constant at 1.15 m in all specimens. A radiodense scale placed at the level of
the bones with the help of small blocks allowed exact measurements (Fig. 2). The
radiographs were transferred to a personal computer and the dimensions of the
bones were measured with a software program (Metron PX™, Epona Tech, Creston,
CA, USA). The lengths of the bones were determined by measuring the distance
between two points that could be exactly defined on the radiographs (Fig. 1 –
longitudinal lines): The longitudinal axis of the cannon bone was determined by first
drawing three lines across the width of the diaphysis of the bone and then drawing a
perpendicular line through the centres of these three lines. At the level of the growth
plate, a line was drawn perpendicularly to the longitudinal axis to serve as a base line
for measuring the length of the cannon bone epiphyses (Fig 1). The length of the
cannon bone epiphyses of the third and fourth digits were measured perpendicularly
to the base line to the condyloid crest. The length of the first phalanx was measured
from the most distal point of its sagittal groove to the most proximal point of the distal
articular surface. The second phalanx was measured from its extensor process to the
most proximal point of the articular surface. The length of the third phalanx was
measured from the extensor process to the tip of the bone. The width of the bones
was determined by measuring a line that ran perpendicularly to the longitudinal line
and through the point of the bone with the largest distance from this line (Fig. 1).
The total length of the third and fourth digit was calculated by adding the lengths
of the single bones of the relevant digits. The lengths of the three phalanges bones
as well as the total digit lengths were compared between the third and the fourth
digit, for the foreleg and the hindleg, respectively, within each species. The width of each bone of the third digit was also compared to the width of the relevant bone of the fourth digit. In addition, the longitudinal axis of the cannon bone was superimposed on the radiographs and extended to the level of the tip of the digits and compared with the axes of the digits (Fig. 1). The dimension of the hoof capsules was determined by measuring three representative variables, i.e., toe length, bulb width and sole width, as described for cattle (Nuss and Paulus, 2006) using callipers with an accuracy of 0.1 mm.

Data are presented as means and standard deviations of measurements of the third and fourth digits of the right and the left limbs. Statistical computations were made using SPSS 11.5 (SPSS Inc. Chicago, IL, USA). Descriptive statistics were used to calculate means and standard deviations. Differences between bone lengths within digits were analysed using a paired t-test. P≤0.05 was considered significant.

Results

There were significant differences in the mean length, and less consistently in the width, of the bones of the third and fourth digits (Table 2 and Table 4). The mean of the length of the cannon bone epiphyses of the fourth digit and the first and second phalanges were all larger than those of the third digit in the front and hind limbs. The mean length of the third phalanx of the third digit was slightly larger than that of the fourth, with the exception of the moose, in which the third phalanx of the fourth digit was longer than that of the third. The mean total length of the fourth digit was greater than that of the third (Table 2). In many specimens, the difference in length was apparent without radiographic examination upon closer examination of the feet (Fig. 2).
In the front limbs, the fourth digit was longer by a mean of 0.5 mm in the chamois, 0.9 mm in the fallow deer, 3.0 mm in the bison and 2.9 mm in the moose. In the hind limbs, the mean difference was 3.0 mm in the chamois, 1.4 mm in the fallow deer, 2.3 mm in the bison and 5.3 mm in the moose (Table 2). Except for the bison, the difference was larger in the hind limbs.

There were also specimens in which the two digits were the same length or the inner digit was longer (Table 2). Overall, the outer digit was longer in 73–95% of the front limbs of all wild ruminant species and in 91–100% of the hind limbs, depending on the species (Table 2). The total length of the digits was larger in the hind limbs than in the front limbs; this difference was largest in the elk (2 cm) and smallest in the bison (2 mm). Age had no effect on the difference in length of the digits of the front and hind limbs.

Comparison of the mean widths of the bones of the forelimbs showed that the epiphysis and the first phalanx of the third digit were wider than those of the fourth digits (Table 3). The width of the second phalanx varied among and within species, and no significant differences were found. However, the third phalanx of the fourth digit was on average wider than the third phalanx of the third digit in all species examined. The differences in bone width were less often significant than the difference in bone length (Table 4). The cannon bone axis, when elongated distally, came closer to the fourth digit in 80% of the 176 front and hind feet. Of the 35 other feet that did not show this pattern, 28 were forelimbs and 7 were hind limbs.

The hoof capsule of the hooves of fourth digits of the hind limbs of wild ruminants was wider because of larger sole and bulb dimensions (Table 4) except in the chamois, where no difference was found. With few exception of the bison, the hoof of the third digit had a longer horn capsule at the toe (dorsal wall length) than its counterpart (Table 4). In the forelimbs the hooves were larger with respect to bulb
width and sole width than in the hind limbs. In one moose kept in a wildlife park and one bison kept in a zoo, the increase in size of the outer hoof was prominent (Fig. 3) and reminiscent of hypertrophic changes commonly seen in domestic cattle. Radiographs of the bison’s feet showed signs of arthrosis and diffuse aseptic pododermatitis, which were more prominent in the hooves of the fourth digits (Fig. 4).

Discussion

The results of this study supported our hypothesis that the fourth digit is usually longer than the third in even-toed ungulates. This has previously been reported in cattle (Muggli, 2007). These findings prompt a careful reassessment of the function of each of the digits during standing and during locomotion.

The radiographic measurements were done in a limited number of even-toed ungulate species that differed in age and gender, and thus, the data do not represent reference values. All fallow deer were intact males one year of age and thus, measurements derived from that group are not representative of fallow deer in general. Similar limitations applied to the claw measurements. However, the primary goal of this study was to investigate possible differences between the fourth and third digits. Because the measurements were done under standardised conditions for both the inner and outer digits, comparisons within animals were justified.

Radiographic measurements usually do not allow exact measurement of bone length because of size changes caused by projection of the radiographic beam on the screen. Schwarzmann identified an error of 3 to 7% in measurement of bone length using radiographs (2005 #7729). Although an error may have occurred in our study, it can be assumed to be much smaller because of the radiodense scale placed at the level of the bones. The scale would have undergone the same proportional change in size as the bones, therefore allowing an accurate measurement of length.
Macerated bones were not used for measurements because the goal of the study was to investigate differences in the length of the outer and inner digits and not to determine absolute bone length. The reference points for the radiographic measurements were identical for the bones of the third and fourth digits and were chosen for their ease of identification rather than to allow measurement of the exact length of the digits. The standardised conditions, use of modern digital equipment and validation of the method (Kummer et al., 2004) ensured that the measurements were reliable and the results comparable.

Our results showed that the paired digits of even-toed ungulates differed in length, and that the outer digit was, in the majority of cases, longer than the inner. This difference was due to the longer metacarpal/metatarsal bone epiphyses and the longer first and second phalanges of the fourth digit (Table 1). The third digit had a slightly longer third phalanx but this did not compensate completely for the difference in total length. The longer third phalanx correlated well with the longer dorsal wall length (toe length) of the hooves of the third digit compared to the hooves of the fourth digits. However, with the exception of the chamois, the outer hooves had significantly wider bulbs and soles in the front limbs as well as the hind limbs. This finding correlated well with the longer outer digit and the wider distal phalanx.

On some of the radiographs, the distal interphalangeal joint of the fourth digit was distinctly angulated, whereas the distal interphalangeal joint of the third digit appeared straighter. This angulation may have caused slight rotation of the third phalanx of the fourth digit, making it appear wider on radiographs. It is not clear whether this angle is present in the live animal or only after death. With high speed cinematography, such a difference could not be seen in cattle walking on a treadmill (Meyer, 2007 #7395){Schmid, 2008 #16845}. We were unable to determine any abnormal conformation that accounted for this digital asymmetry.
A difference in the total length of the digits was observed in more than 91% of hind limbs and in more than 73% of the forelimbs, similar to reports in domestic ruminants (Schwarzmann, 2005; Muggli, 2007). Age had no apparent effect on the difference in length of the paired digits in this study and in studies of ruminants (Schwarzmann, 2005; Muggli, 2007). Thus, it can be assumed that the length difference is a characteristic of artiodactyls, and that it possibly originated from a common ancestor with the same trait. It is reasonable to assume that the difference in length of the paired digits is the result of an evolutionary selection process that was advantageous to the animal.

A small number of the animals in our study had inner digits that were equal to or longer than the outer ones. It can be speculated that in the evolutionary process, a small percentage of individuals deviate from the norm so that adaptation to sudden changes in the environment and thus, preservation of a species, may be better assured.

There are several reasons why a difference in digit length and width could be adaptive for ruminants. The centre of gravity, located in the middle of the trunk of quadrupeds, is stabilised by longer outer digits, particularly on soft ground. In wild ruminants, the outer hoof was wider than the inner in the front and hind limbs; this difference was less distinct in ruminants kept in smaller enclosures (Fig. 3) or in domestic cattle (Nuss and Paulus, 2006). We hypothesise that the fourth digit serves to stabilise the centre of gravity to a greater extent than to bear weight, whereas the opposite applies to the third digit. In one heifer it was shown that on soft ground, the hoof of the third digit of a front limb absorbed an impact force higher than the fourth digit (Seebacher et al., 1980). If this was true for a larger number of animals, it would explain why the mean widths of the third metapodial epiphysis and the first phalanx of the third digit are larger (Bartosiewicz et al., 1997).
Under natural conditions, asymmetric digits and larger outer hooves may provide an advantage in terms of stability, because the longer outer digit provides better contact with the ground during movement and better stability while standing. It might be speculated that, when pushing forward, for example during a fight with a rival, the hind limbs are positioned at an outward angle which necessitates longer outer digits to maintain ground contact. When climbing a slope or during a quick turn to escape a predator, longer outer digits can be advantageous for the same reason. Spreading of the digits per se increases contact and frictional area and prevents slipping (Manning et al., 1990). The advantages of asymmetric digits and hooves may have contributed to the wide distribution of artiodactyls in different habitats such as alpine (chamois), marshy (moose), forest (fallow deer) and prairie (bison) environments.

A prevailing deviation in the direction of the foot axis was seen in wild ruminants, in which the axis of the cannon bone ran closer to the outer digit (Fig. 1). The incongruity between the axes of the cannon bone and the digits could possibly be caused by a deviation of the cannon bone axis at the level of the epiphyseal groove. In domestic cattle, such a clear-cut deviation of the limb axis could not be seen (Muggli, 2007). Measurement of the cannon bone axis should therefore be repeated using specimens in which the entire length of the cannon bone is seen on radiographs.

The anatomical differences identified in our study may aid in the interpretation of degenerative bone lesions and the differentiation of bone fragments in biological and archaeological specimens. The metapodia of modern ruminants differ only in size and not in anatomical proportion compared with their ancestors (Paral et al., 2004). Despite the disadvantages incurred by domestic ruminants kept in small enclosures and on hard surfaces during their domestication, the structural principles of the bones of the digits have not changed (Muggli, 2007). However, in domestic cattle, the
natural selection processes have been disturbed by breeding programs and management interventions, such as claw trimming, a main goal of which is to eliminate asymmetries. The hoof capsules of the hooves of the fourth digits were wider as evidenced by larger sole and bulb dimensions (Table 4). The horn capsules of the hooves of the front limbs were larger than in the hind limbs, presumably because the centre of gravity is closer to the front limbs. Except for moose, the dorsal wall was longer in the forelimbs than in the hind limbs; such differences among species may be related to the species' habitat and require further investigation. Of special interest is also the question of whether the asymmetry of paired claws is related to a difference in the loads the two digits are subjected to.

In summary, our results showed significant differences in the length of the paired digits and hooves of even-toed ungulates. Whether and to what degree these differences are accompanied by corresponding differences in soft tissue structures and function requires further study. On hard surfaces, these anatomical differences may lead to hypertrophy and deformation of the outer hoof, which is evident in domestic cattle as well as in wild artiodactyls kept in captivity.

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References


