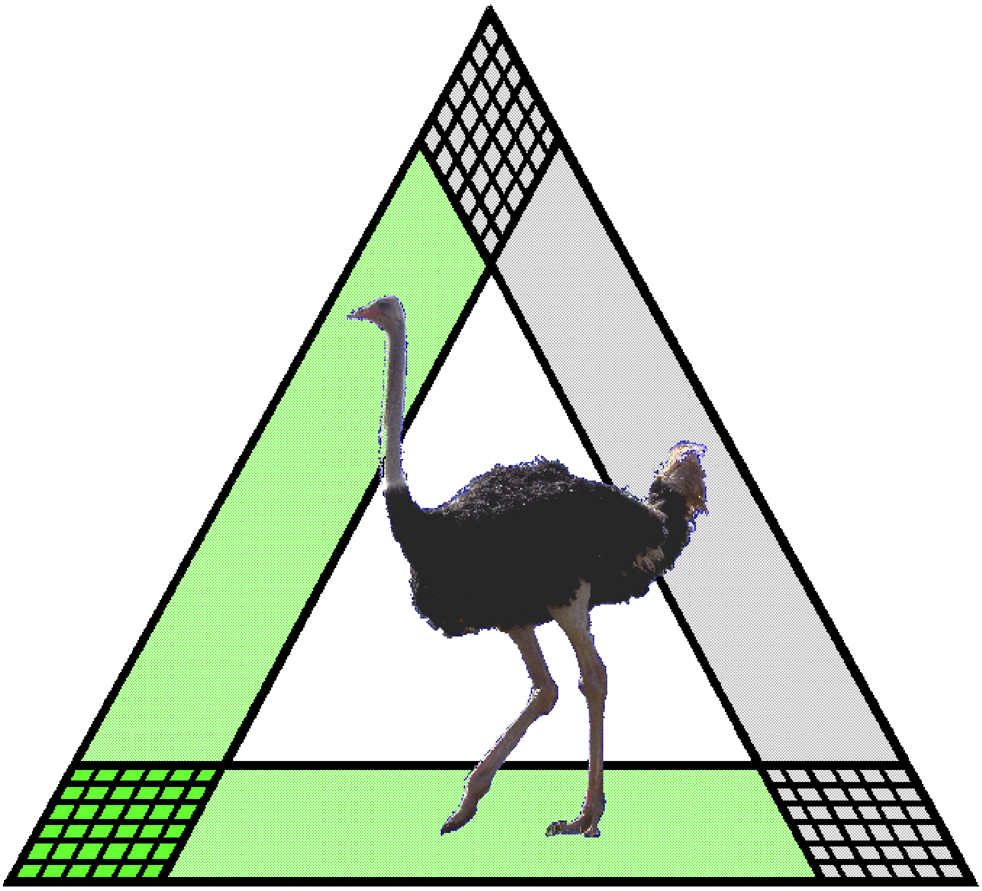

Structural attributes contributing to locomotor performance in the ostrich

Nina U. Schaller
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Structural attributes contributing to locomotor performance in the ostrich (*Struthio camelus*)

presented by
Dipl. Biol. Nina U. Schaller
Birthplace: Kronberg/Ts (Germany)
Oral examination: 16th October 2008

Referees: Prof. Dr.Dr. hc. Volker Storch

Prof. Dr. Thomas Braunbeck

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Appendix

A Acknowledgements

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B Summary

As the fastest long-endurance runner, the bipedal ostrich (*Struthio camelus*) was selected as a prime model organism to investigate the physical attributes underlying this advanced locomotor performance. A specific integrative approach combining morphological, morphometric, kinematic and pedobarographic methods was developed.

The comparative morphometric analysis of the hind limbs of all ratite species revealed that leg segment ratios in the ostrich are the most specialised for efficient locomotion, especially when taking into consideration its unique supra-jointed toe posture. In addition, the crural muscle mass is more concentrated towards the hip joint in the ostrich than in its ratite relatives. According to the Law of the Pendulum, this concentration of mass towards the pivot point – in concert with the relatively longest and lightest distal leg elements – represents a mechanical optimisation of limb swinging capacities.

While musculature clearly drives limb movement, the passive guidance and constraint of motion range by ligamentous structures combined with joint surface contours allows a high level of energy output efficiency during all stages of locomotion and ensures articular stability during slow locomotion as well as high-speed performance. So far, the influence of these passive effects in locomotion has been largely ignored. In order to quantify the guiding effect of these anatomical structures, kinematic data of adult ostriches during walking and running were collected. Subsequently, these data were compared with results from manual manipulation experiments performed with the limbs of anatomical specimens – both fully intact and with muscles removed – leaving only the ligament system intact. This investigation revealed that the range of motion among leg segments was nearly identical in all sample groups, especially in regard to maximum extension values. This indicates that ostrich hind limb dynamics are managed to a significant degree by passive elements that ensure a controlled swing-plane with minimal deviation from an optimal attitude. Further dissections allowed some of these features to be described in detail, with an emphasis on functional-morphological examination of the intertarsal joint. The intertarsal joint contains a significant locking mechanism, briefly mentioned in historical documents, but described and functionally analysed herein for the first time. The functional examination qualified the interplay of three collateral ligaments, the tendinous M. fibularis brevis and specific joint surface protrusions as the basis for this effect which remains absent in smaller ground-dwelling bird species. A proximate quantification, based on comparative morphological and kinematic data, revealed function of *Struthio*'s passively locked intertarsal joint as a potent stabiliser in the supporting limb during the ground-contact phase of locomotion.

During stance phase, it is crucial that the supporting limb is stabilised internally and in relation to the substrate. As yet, no study exists concerning use and loading of the actual ground contact elements. The toes must absorb body mass, guarantee stable grip and provide energetic push off. Obvious specialisations of the ostrich's phalangeal complex include toe reduction (leaving only 3rd and 4th toe), claw reduction (only at 3rd toe) and a permanently elevated metatarsophalangeal joint. Using a relatively new methodology to examine *in vivo* toe function, pedobarography was employed on specifically trained ostriches to allow extensive collection of Centre of Pressure (CoP) and load distribution (LD) data. In contrast to a relatively predictable CoP trajectory at all speeds, conspicuous LD differences were observed between slow and fast trials. Load was distributed rather inconsistently during walking, while a typical tripod-like toe-print occurred in all running trials to presumably deliver additional stability during the comparatively short stance phase. Significant grip is provided by the highly directed impact of the 3rd toe claw-tip, suggesting its important function as a positional anchor during running. Pedobarographic analysis further showed the importance of the 4th toe as an outrigger to maintain balance, rendering a future reduction highly unlikely.

In conclusion, the application of interdisciplinary methodologies allowed comprehensive data collection and integration of the model organism within its ecological context. The data gained from this thesis increases the current knowledge about ostrich locomotion by identifying distinct structural attributes as essential elements for extreme cursorial performance. The present data may alter existing models for calculation of the metabolic cost of terrestrial locomotion and aid in the reconstruction of theropod locomotion, as these branch sciences often overlook the important role of ligaments and passively-coupled motion cycles in reducing the cost of locomotion.

C Zusammenfassung

Der Afrikanische Strauß (*Struthio camelus*) stellt den effektivsten Typ eines Hochleistungsdauerläufers dar und erreicht Spitzengeschwindigkeiten von 80 kmh^{-1}. Im Rahmen eines integrativen Ansatzes wurde durch Verknüpfung ausgewählter Methoden morphologischer und biomechanischer Disziplinen ein umfassendes Erklärungsmodell für diese Form der Dauerlokomotion erstellt. Speziell strukturelle Besonderheiten innerhalb der Konstruktion Strauß standen im Mittelpunkt der Untersuchungen.

Beim Vergleich des statischen Aufbaus verschiedener Bipedietypen fiel beim eher schweren Strauß die zentrische Auflagerung des langen, horizontal ausgerichteten Körpers auf einem weitgehend vertikal orientierten Bein auf, wobei die auf die distalen Gelenke wirkenden Drehmomente minimal bleiben, was kompensierende Muskelkraft minimiert. Durch die vogeltypische Horizontalstellung des Femur treten zwar Flexionsmomente in Knie und Hüfte auf; diese werden aber strukturell durch das im Vergleich mit anderen Vogelarten relativ kurze Femur bzw. Hebelarm, reduziert und durch stringente Ligamentaufhängung zudem abgefangen. Zusätzliche Stabilität der langen Gliedmaßen wird bewirkt durch ein ratitenspezifisches Hebelsystem von am proximalen Tibiotarsus kranial und am proximalen Tarsometatarsus kaudal ausgerichteten knöchernen Processi. Über diese verläuft ein beim Strauß extrem ausgeprägtes mehrgelenkiges Muskel-Sehnensystem, das funktionell Becken mit Zehen verbindet, und in stehender Position der Beinarretierung dient und damit energiearmes Stehen erleichtert. Die Gelenkanalyse ergab zudem, dass das Intertarsalgelenk, welches sich fast genau in der Mitte des vertikal orientierten Beins befindet, durch einen bändergesteuerten Einrastmechanismus stabilisiert wird, der sowohl Überbeugung als auch Überstrecken verhindert. Bezüglich der Betrachtung der Lokomotionsdynamik ergab der morphologisch-morphometrische Vergleich verschiedener kursorialer Vogelarten, dass der Strauß optimale mechanische Pendeleigenschaften seiner Extremität aufweist bedingt durch Proximalverlagerung seiner Antriebsmuskulatur hin zum Becken mit kurzem Femur (s.o.), wobei das frei schwingende Bein effektiv am längsten und leichtesten ist. Dies wird nicht nur durch Verlängerung von Tibiotarsus und Tarsometatarsus erreicht, sondern auch durch das bei keinem anderen Vogel auftretende permanente Abheben des proximalen Zehensegments, und damit Metatarsophalangengelenks, vom Substrat. Bei Pro- und Retraktion des langen Beins werden alle Segmente gekoppelt über lange Sehnen des mehrgelenkigen Muskel-Sehnensystems bewegt, wobei die Sehnen der Zehenflexoren über das spezifisch abgehobene Metatarsophalangengelenk verlaufen womit bei dessen Beugung/Auffußen elastische Energie in Sehnen gespeichert und beim Strecken/Abfußen wieder abgegeben wird. Diese Energierückgewinnung stellt einen entscheidender Faktor für effektive Dauerlokomotion dar. Die Gelenkanalyse zeigte zudem, dass laterale Freiheitsgrade größtenteils passiv über Form- und Bänderführung limitiert werden, also nur in eingeschränktem Maße über Muskelkraft kontrolliert werden müssen, was metabolisch erzeugte Energie spart. Dadurch wird die proximal erzeugte Kraft direkt in die für das Erzielen großer Schrittweiten wichtige und energetisch aufwendige Protraktion des Beins geleitet, wobei die Leistungskraft der Hüft- und Knieextensoren über die Hebelwirkung der kranial verlängerten Crista cnemialis cranialis noch verstärkt wird. Vor dem Auffußen führt die gekoppelte Beinbewegung automatisch zur Streckung aller Gelenke mit Abduktion der vierten Zehe. Die erstmals an Straußen durchgeführte pedobarographische Analyse zeigte, dass effektives Abbremsen des beim Rennen hoch beschleunigten Schwungbeins zu Beginn der Standbeinphase durch die prominente Klaue der dritten Zehe gewährleistet wird, die sich förmlich in das Substrat bohrt. Der bei schneller Lokomotion auf die Zehen einwirkende Druck wird im proximalen Bereich der dritten Zehe und somit nah am Metatarsophalangengelenk konzentriert, was die auf dieses Gelenk wirkenden Drehmomente relativ gering hält und somit als weitere Strategie zur Einsparung gelenkstabilisierender Muskulatur interpretiert wurde. Wie Untersuchung von Gesamtkörperstatik und Zehenfunktion zeigten, kann die vierte Zehe – im Gegensatz zu den quadrupeden Equiden – nicht reduziert werden, da für den bipeden Strauß diese lateral ausgerichtete Zehe eine entscheidende Balancierfunktion während Stand, gehender und rennender Fortbewegung erfüllt. In diesem Zusammenhang steht auch die hier gemachte Beobachtung, dass die Flügel des flugunfähigen Straußes entgegen bestehender Meinung bei der terrestrischen Fortbewegung als Balancier- und „Abbremshilfe“ eine entscheidende Rolle spielen.

Es wird festgehalten, dass die durch integrative Analyse gefundenen strukturellen Attribute maßgeblich zum Verständnis der außerordentlichen Laufleistung des Strauß beigetragen haben.

1 Introduction

Mobility is a crucial component in an organism's acquisition of nutrition, pursuit of reproductive opportunities or evasion of predators. In an evolutionary context, the ability to migrate may determine whether a species survives or vanishes in the face of changing environmental conditions. Mobility is achieved in a number of ways. Animals – evertebrates and vertebrates alike – exhibit a wide range of locomotor behaviour including swimming, flying, climbing, hopping, jumping, walking and running on two, four, six, eight or more legs. This diversity is taken to an extreme by penguins "flying" underwater and flying fish "gliding" through air.

When comparing energy requirements for aerial, aquatic and terrestrial mobility among vertebrates, it can be generally stated that terrestrial – especially pedal – locomotion consumes the most energy. A higher quantity of joules are required to transport 1 kg of body mass 1 metre within a given period on the ground than in water or air (e.g. Tucker, 1973, 1975). Hence, it can be expected that the *bauplan* of a vertebrate species relying exclusively on this comparatively costly mode of locomotion incorporates structural and metabolic specialisations that effectively transform energy into mobility. This is of particular interest in the ostrich, wherein an avian species has abandoned its flying abilities in favour of a terrestrial lifestyle. Although this study does not purport to offer explanations regarding this transformation, the earthbound status of the ostrich provides the essential context for this research.

Scientists have explored the challenges of terrestrial locomotion in detail including investigation of relevant muscle groups, physiological specialisations, enzyme activities and biomechanical analyses of overall body movement or distinct skeletal elements (e.g. Alexander & Jayes, 1978; Alexander, 1984; Minetti, 1998; Muybridge, 1887; Preuschoft, 1979; Roberts et al., 1998a; Schmidt-Nielsen, 1972; Stolpe, 1932; Taylor, 1977). A wealth of data concerning human bipedality has been compiled, largely influencing methodological developments and further defining the principles of bipedal locomotion (e.g. Brinckmann et al., 2000; Liu & Nigg, 2000, Lugné et al., 1999; Moritz & Farley, 2005; Pontzer, 2005; Vaughan, 2003). In addition, mammalian terrestrial locomotion has been studied with particular emphasis on domesticated animals like horses and dogs (e.g. Magne de la Croix, 1936; Minetti et al., 1999; Morgan et al., 1978).

Studies on avian locomotor modes have typically explored flight dynamics (e.g. Pennycuick, 1975; Rayner, 1995). However, avian species manifest a wide range of locomotor abilities (walking, running, hopping, swimming, diving, flying, gliding) due to a functional de-coupling of fore and hind limbs that persists as a heritage of their theropod ancestry. This group of dinosaurs used only their hind limbs for locomotion allowing the subsequent evolutionary development of the forelimbs for flight. With the advent of modern technologies, terrestrial locomotor modes in avian species are now receiving increased attention from various disciplines, complementing the existing data pool of four-legged and human locomotion (e.g. Verstappen et al., 2000; Ellerby & Marsh, 2006; Gabaldon et al., 2004).

To-date, the majority of studies examining avian terrestrial locomotion were either focused on anatomical specimens or, when investigating live subjects, were carried out under laboratory conditions. These experiments sometimes required physical manipulation that may have affected natural motion range and results (e.g. Nassar et al., 2001).

Due to methodological restrictions and handling convenience, smaller species such as Guinea fowl (*Numida meleagris*), quail (*Coturnix* sp.) and turkeys (*Meleagris gallopavo*) were often chosen as the subjects for investigation (e.g. Clark & Alexander, 1975; Gatesy, 1999; Roberts et al., 1998b).

An optimum strategy in the study of avian pedal locomotion is the investigation of an organism that exhibits an apparent adaptation to this particular modality, employing walking and running as its default option for covering distances. As opposed to birds which retain the option to fly, flightless species possess a metabolism and *bauplan* specifically adapted to a terrestrial lifestyle. Since all Struthioniformes have lost the ability to fly, ostriches (*Struthio camelus*), rheas (*Rhea americana* and *Pterocnemia pennata*) emu (*Dromaius novaehollandiae*), cassowaries (*Casuarius* sp.) and kiwis (*Apteryx* sp.) serve as ideal model organisms.

Ostriches in particular are acknowledged as excellent long-endurance runners, capable of running with a speed of 60 km/h for durations exceeding twenty minutes while reaching peak velocities up to 80 km/h – surpassing the locomotor abilities of their ratite relatives. Documentation of this performance is presented by Alexander et al. (1979), Hallam (1992) and can be seen in Grzimek's documentary "Serengeti Shall Not Die" (1959). When not running, ostriches spend their waking hours in near-constant motion or standing interrupted only by brief periods of sitting or bathing/preening in sand (Bertram, 1992). In consideration of this near-constant locomotor behaviour, one can expect that the pelvic limb of the ostrich exhibits special features adapted to this mobile lifestyle, especially since the legs of this largest extant biped support a body mass ranging from 90 to 170 kg (Deeming, 1999). Male adults in Kenya inhabit territories between 11 and 19 km^2 and female birds cover a larger average range of at least 25 km^2 migrating among the territories of various males. Both genders spend one third of daylight time travelling and an equal amount of time feeding (Bertram, 1992; Williams et al., 1993). In its native semi-arid environment, efficient locomotion is essential to survival in order to access scarce sources of food and water. With a lifespan of up to 85 years and daily activity time of 13 hours, the ostrich has been selected as a model for the study of bipedal locomotor behaviour.

The aim of this study is to undertake a comprehensive assessment of the advanced locomotor abilities of the ostrich and describe structural attributes of the locomotor apparatus that enable this extreme level of performance. To provide both proximate (mechanistic & bodily) and ultimate (evolutionary & environmental) understanding of performance, this bird must be appreciated as a unity of finely tuned subsystems which function in a highly co-ordinated manner. By definition, locomotion results from directed deformation of an organism by musculature. This deformation is directed internally towards skeletal elements and externally towards the substrate to convert motion into locomotion. In the ostrich, physiological and physical modifications towards fast long-endurance locomotion include:

Metabolic refinements: An effective lung for maximum oxygen intake, an efficient digestive system coupled with specific blood composition and a powerful heart controlled by a tuned CNS driving the musculoskeletal complex.

Mechanical refinements: Balanced interaction of musculature with the skeleton and efficiency of the swinging pendulum of the limb with short proximal skeletal elements supporting the primary locomotor muscle mass and long, light distal skeletal elements.

Structural/Histological properties: Muscles possess a particular ratio of slow and fast fibres in specific muscle groups acting on skeletal elements of a suitable bone density. To conserve energy during high speed running, muscles and particularly their tendons store and reflect elastic energy.

Passive structures and automated chains of motion: In addition to active elements (i.e. muscles) which direct movement by using metabolic energy, passive elements (i.e. ligaments, cartilage, joint morphometry) must also be considered in the context of mobility. Passive systems can provide locomotor benefits and increase overall efficiency without increasing metabolic energy consumption.

Naturally, these interwoven systems are of equal importance to the overall success of the organism. Increased comprehension of ostrich locomotion can be achieved by applying an integrative approach where proximate and ultimate coherence is assessed, with subsequent methodological isolation of each subsystem for targeted analyses (e.g. Herkner, 1999). Practically speaking, it is impossible to comprehend any organism in its totality, and one is forced to define the parameters of an inquiry to increase the likelihood of making reasonable progress towards a given aim. However, any specific insight or observation viewed in isolation must subsequently be reintegrated – methodologically and theoretically – into the larger view of the subject as a functioning entity. This ethos allows the opportunity to explore, distil and reconstitute information to derive an evolving and accurate description of a bio-system within its environmental context.

To-date, it has been common procedure to extract individual data in separate experiments, often preventing a holistic understanding of ostrich locomotion. In order to close some of the existing gaps in understanding, this study employs a range of methods to obtain relevant data that reflects the natural range of motion and behaviour of the subject. The specific application of this approach is detailed in Chapter 3.1 (Materials & methods) where morphological and biomechanical methods are employed in a concerted manner to determine structural attributes contributing to ostrich locomotor performance.

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2 State of present knowledge and basic principles

This chapter presents a state-of-the-art itemisation of physical and physiological systems involved in efficient locomotion and includes a summary of evolutionary background and metabolic refinements of the ostrich. The basic principles of statics and dynamics are referenced in the context of structural specialisations for economic locomotion. Specific literature referring to anatomy, morphology, behaviour and biomechanics are listed in the respective chapters throughout this study.

2.1 Classification and evolutionary background

Ostriches (*Struthionidae*) are subdivided into five subspecies: the extant *S. c. camelus*, *S. c. molybdophanes*, *S. c. massaicus*, *S. c. australis* and *S. c. syriacus* of the Syrian desert which was hunted to extinction during World War II. The families of ostriches, rheas (*Rheidae*, South America), cassowaries (*Casuariidae*, New Guinea and Northwest Australia) and kiwis (*Apterygidae*, New Zealand) form the order Struthioniformes. Adding the extinct moas of New Zealand (Dinornithiformes) and the elephant birds of Madagascar (Aepyornithiformes) completes the group ratites. This name is derived from the Latin 'ratis', a keel-less boat, since this group of birds does not possess a carina (the sternal elongation at which a large part of the pectoral flight muscles originate). The ratites and the South American tinamous all show a distinct anatomy of their palatium which, in addition to the absent carina, is used to separate this group from the Neognathae (practically all other bird species) into the subclass Palaeognathae within the class Aves (e.g. Del Hoyo et al., 1992).

The origin of the Palaeognathae remains a topic of debate (e.g. Glutz von Blotzheim, 1958; Gussekloo, 2000; Kälin, 1942; Lowe, 1928; Lutz, 1942). As proposed by the functional-morphological analyses of de Beer (1957), ratites descended from volant ancestors. Their particular palatium is not a primitive characteristic but is instead a neotene feature and represents an early stage of carinate ontogeny (de Beer, 1957). Other neotene ratite characteristics include down-like plumage and preservation of sutures of the skull. Despite their parallel use of a functional-morphological methodology, Houde & Olson (1981) argue that the Palaeognathae are in fact primordial and therefore form a monophyletic group. However, most scientists in this field follow the hypothesis of de Beer (1957) and agree that ratites once had, and subsequently lost, the ability to fly (e.g. Olson, 1985).

While the composition of ratite species as one group is widely accepted, the degree of inter-relationship remains unclear despite – or perhaps because of – the employment of a wide range of methodologies (e.g. Krampitz et al., 1974; Oberthür et al., 1983; Silyn-Roberts & Sharp, 1985). Even the evolutionary background of *Struthio* is still debated. Recent data indicate that this species evolved during the Miocene (26–7 MYA) in Africa and migrated to Eurasia around 10-5 MYA (Mourer-Chauviré et al., 1996a,b). Olson (1985), on the other hand, suggests that ostriches could have evolved in Eurasia from crane-like ancestors, the Enantiornithes, from the early Oligocene to the Pliocene. Like the ostrich, *Ergilornis rapidus* and *Amphipelargus* were didactyle flightless cursorial birds and lived in a similar steppe-like environment. Houde & Olson (1981) place the three-toed *Paleotis weigelti*, discovered at the Messel pit near Darmstadt, Germany, in the line of struthionid ancestors. Whether the Ergilornithidae belong to the ancestral line of *Struthio* or the Gruiformes (cranes) is still a matter of discussion. By contrast, Peters (1988) concluded that *Paleotis* rather belongs to the *Rheidae*.

Of interest to the present study is the potential connection between ostrich and theropod locomotion. This possible cross-referencing can be especially useful in the reconstruction of these animals from fossil remains and shed additional light on interpretations of their locomotor patterns and lifestyles (Gatesy, 1990). Despite ranging from chicken-sized to elephantine, all carnivore theropods presumably employed similar locomotor behaviour as digitigrade, parasagitally striding bipeds (Farlow et al. 2000; Paul, 1998). However, theropods had a long, heavy tail that acted as a counterbalance. Modern birds reduced the tail while simultaneously elongating the tarsometatarsus to compensate for this missing counterbalancing structure (Gatesy, 1995; Gatesy & Middleton, 1997).

In theropod dinosaurs, as in crocodilians and squamata, the M. caudofemoralis served as the main retractor of the femur running along the caudal vertebral column (e.g. personal communication, Herkner, 2008). With this muscle working as a femoral retractor/hip extensor, the tail, as its major area of origin, cannot be reduced. A long tail can be reduced if propulsion is no longer coupled to femoral retraction but is instead induced mainly by distal limb retraction (from the knee downwards) as seen in avian species. In an evolutionary context, the shift of propulsive action towards the distal limb elements involved reducing the length of the femur and positioning it horizontally. Fossil evidence for this trend is widely available. The reorientation of femur position from predominantly vertical to horizontal occurred concurrently with a cranial shift of the Center of Mass (CoM) due to the reduction of the tail and, consequently, the mass of the M. caudofemoralis attached to it. Theropods occupying the evolutionary transition zone to avian species possessed light, stick-like tails which no longer carried propulsive musculature but were instead employed as balancing tools during turning manoeuvres. If this balancing function is assumed by other structures, like long tail feathers and/or extended wings, the tail can be fully reduced as seen in the theropod Caudipteryx.

2.2 General physiology – Metabolic refinements for economic cost of transport

Respiration

The avian respiratory system shows distinct differences from the mammalian one. The avian breathing apparatus does not simply inhale air and then expel it, but instead provides unidirectional flow of air into the lungs and body, circulating the air through a series of large sacs and hollow bones (Duncker, 1978; Schmidt-Nielsen, 1971). The ostrich possesses a lung/air sac system consisting of ten air sacs reaching from head to abdomen and continuing into the femora (Bezuidenhout, 1998). Skadhauge & Dawson (1999) measured a tidal volume of 15 l in an ostrich with a body mass of 100 kg. By comparison, the average tidal volume for humans is 3 to 4 l, with maximum volumes up to 7 l measured in athletes (Adegoke & Arogundade, 2002; Doherty & Dimitriou, 1997). Maina & Nathaniel (2001) proved that ostrich lung efficiency is at least equal to that of migrating geese, thereby mitigating oxygen debt during episodes of extended terrestrial locomotion. The lung system of cursorial avian species provides interesting subject matter relating to locomotor adaptations in light of findings that the locomotor and ventilatory cycles are coordinated and could economise running performance (Bramble & Carrier, 1983). To achieve this benefit, the resonant frequency of the respiratory system would be coupled to, and modulated by, the preferred stride frequency of the animal. This appears to be the case in the guinea fowl (*Numida meleagris*) (Nassar et al., 2001) and would, by extension, prove beneficial to the long-endurance ostrich.

The ventilatory system of ratites has been used as a model for reconstruction of the theropod respiratory system to explore the divergent evolution of mammalian and avian lung morphology (Claessens, 2004; Perry, 1992, 2001). In the context of the present study, it is very interesting to note that some researchers propose a correlation between the evolution of the respiratory system and development towards bipedal locomotion (Carrier & Farmer 2000; Hicks et al., 1998).

Metabolism

In addition to the established understanding of avian physiology (e.g. Peaker, 1975), a range of data is available concerning metabolic data of ratites and ostriches in particular (e.g. Cloudley-Thompson & Mohamed, 1967). From a physiological standpoint, the status of the ostrich as the largest and heaviest extant bird ensures its relatively economic metabolic cost of locomotion since the cost of transporting 1 kg of body mass per meter decreases as body mass increases (Heglund et al., 1982 a,b; Taylor et al., 1970; Taylor, 1977; Taylor et al., 1980).

Interestingly, the Basal Metabolic Rate (BMR) of ostriches (0.113 ml Oxygen g^{-1} h^{-1}) is only 58% of the value predicted for a 100 kg non-passerine bird (Withers, 1983). This data may reflect the physiological advantage of being 'big' based on the fact that “large birds use more energy than small birds in absolute terms but less per unit mass” (Skadhauge & Dawson, 1999). However, the maximum factorial scope is at least 28 times the BMR (Withers, 1983), and may exceed this level in feral ostriches. The low BMR and the ability to rapidly increase metabolic rate as required to meet energy demands suggests another factor in this bird’s exceptional locomotor abilities.

Energetics and power output of certain muscle groups in accelerating, de-/incline and steady running birds has been studied for a number of species ranging from quail to ratites (e.g. Fedak et al., 1974; Fedak et al., 1982; Gabaldon et al., 2004; Heglund et al., 1982 a, b; Roberts et al., 1997; Roberts et al., 1998; Roberts & Scales, 2002; Taylor, 1977; Taylor et al., 1982).

Amongst others, Roberts et al. (1997; 1998) compared quadrupedal to bipedal locomotion and found that birds consume 1.7 times the amount of metabolic energy for any given rate of force production. Conversely, step lengths are longer in birds to allow the exertion of more power at a given speed. As a consequence, the horse and ostrich appear to have nearly the same relative cost of transport in running (Fedak & Seeherman, 1979).

Blood chemistry data is available in DeVilliers (1938) and Perleman (1999) and specific haematological data for resting ostriches can be found in Levy et al. (1989). However, no studies were found that indicate blood chemistry adaptations to sustain high activity levels.

Digestive system and feeding

Adult birds are able to extract water from succulent plants, allowing independence from water holes and ensuring a large activity radius (Williams et al., 1993). Contrary to some reports that suggest ingestion of insects and lizards, the diet of the ostrich is restricted to plant matter (Deeming & Bubier, 1999; Milton et al., 1994) subsequently processed by the most efficient post-gastric fibre fermentation system amongst birds (Cilliers & Angel, 1999; Scheideler & Angel, 1994) to absorb food energy with the highest cost/benefit ratio.

Thermoregulation

The ostrich possesses several adaptations towards life in a semi-arid habitat with typically high solar radiation. A behavioural response to momentary heat stress, besides seeking shade, is to erect feathers and expose areas of bare skin by abducting the wings. This effect is increased by turning in the direction of prevailing wind as observed numerous times in the birds used for this study. If wind provides no relief, the birds will pant by accelerating respiration frequency from 4 (the lowest in all birds) to 40 - 50 breaths min^{-1} (BPM), thereby increasing ventilation and the resultant cooling effects without increasing oxygen intake (Skadhauge & Dawson, 1999). In rainy or cold weather, these techniques are reversed and skin is covered using plumage and wings. Heat conservation is maximised when sitting and extremities are protected from the elements.

Comparative data about physiological thermoregulatory strategies of ratites and several other avian species have been presented by Dawson et al. (1983) and Maloney & Dawson (1994). During long-term heat exposure (> 50°C) with the resultant effect of dehydration, ostriches can increase body temperature by 4°C from an average 39°C, the lowest basal temperature amongst birds. Simultaneously, respiratory frequency halves to approximately 25 bpm, resulting in a significant reduction in evaporation rate (Crawford & Schmidt-Nielsen, 1967). Evaporative water loss is also managed through the expiration of unsaturated air (Withers et al., 1981) by establishing a temperature gradient along the trachea (Schmidt-Nielsen et al., 1969). Withers (1983) found that ostriches are able to conserve 200–500 ml of water per day, representing a significant proportion considering a minimum water turnover of 2 l day^{-1} (Skadhauge & Dawson, 1999). Analyses based on infrared-thermographic data reported that ostriches regulate their body surface temperature more effectively than the related emu or cassowary (Phillips & Sanborn, 1994).

Sensory organ - eye

The eye of the ostrich is the largest amongst all extant terrestrial vertebrates with an average diameter of 50 mm (King & McLelland, 1984). Like other avian species, ostriches have excellent eyesight. The visual fields of the ostrich are rather narrow when compared to other birds, but a highly mobile neck effectively compensates for this limitation (Martin & Katzir, 1996). Ostriches have a large blind spot above and behind the head that may be a consequence of the eyelids and eyelash-like feathers required to protect eyes from sunlight and airborne particulate matter.

2.3 Statics and dynamics - General strategies and structural specialisations for economic locomotion

The following overview presents general strategies that allow efficient standing, walking and running in accordance with the hypothesis of this study that the ostrich possesses structural attributes optimised to its cursorial locomotor behaviour.

A body is statically stable when it is capable of supporting itself and seeks to achieve a maximum degree of static stability with the least material (Kummer, 1956). Three primary elements of a system's construction must contribute to maintenance of static equilibrium (Kummer, 1956):

- Bracing of the entire body, particularly trunk and vertebral column, *via* muscles, tendons and ligaments
- Orientation and balance of internal/external forces through the free extremities, particularly the long bones of the limbs
- Structure of the cancellous bone, particularly at the coaxial end of the femur

The entire body and extremities must be braced by muscles, tendons and ligaments to ensure internal integrity. Depending on the orientation of extremities and areas of muscle origin, load –and, to a higher degree, bending forces – act on the skeletal scaffolding (e.g. Kummer, 1956). In order to equally distribute the forces resulting from body mass, a bipedal organism arranges its trunk on top of two predominantly vertical columns (e.g. Kummer 1956; see **Fig.** 2.3.**1**: Biped).

In a live organism the limbs are articulated *via* joints, classified into different types, where a simple hinge joint exhibits only one degree of freedom while a ball-and-socket joint may exhibit eight degrees of freedom (Bögelsack et al., 2000). For example, the intertarsal joint of the ostrich – as the functional analogue to the human knee – is not a simple hinge joint but can achieve more than one degree of freedom by means of incongruent joint surfaces that further incorporate roll-and-glide capacities. A wealth of studies exist concerning joint mechanics and include great detail regarding technical, anatomical, orthopaedic and even philosophical aspects with some older monographs concentrating specifically on avian hind limb articulation (e.g. Bögelsack et al., 2000; Blickhan et al., 2007; Bell, 1849; Hultkrantz, 1897; Langer, 1857; Menschik, 1987; Stolpe, 1932). A recent study explores the forces present at the hip joint of the emu in great detail, further underlining the importance of this joint in overall maintenance of posture and balance (Goetz et. al, 2008).

Depending on the relative orientation of limb segments and the resulting force vectors exerted by body mass, torque moments also act on the involved joint. To control the resulting moments acting on the limb structures and joints, an organism possesses stabilising musculature and adjusts limb posture as required. In *Homo sapiens*, an advantageous body posture is achieved by standing with the knee fully extended to provide columnar support for the vertically positioned trunk. In a biped of similar mass but different physiognomy, the intertarsal joint of the ostrich is extended with identical purpose. However, the major static difference between the ostrich and human form is that the ostrich trunk/vertebral column and femur are oriented nearly horizontally, reflecting typical avian construction. Potentially disadvantageous flexing moments acting on the hip resulting from this overall horizontal orientation are alleviated by the relatively short femur providing a corresponding reduction in moments at this joint (e.g. Gatesy, 1990). Within these two expressions of bipedalism, variations in overall dimension and mass affect the position of the Centre of Mass (CoM), (e.g. Vogel, 2003), and also result in differences in the distance between CoM and the substrate (Chapter 4.1.3). Both factors affect overall static equilibrium to a significant degree.

In addition to the basic parameters of limb posture, additional strategies for stable bipedal standing are established by neural and motor control combined with appropriately sized feet/ground contact surfaces to establish a suitable Base of Support (BoS). The essential precondition for balanced standing is that the vertical projection of the Centre of Mass must always be contained within the BoS (e.g. Hof, 2008). This can include a certain degree of tilting, as long as the perpendicular of the CoM remains within the BoS (e.g. Kummer, 1956).

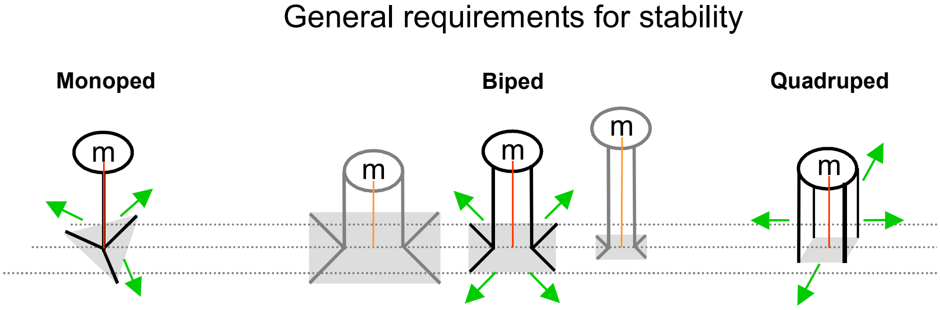

Fig. 2.3.**1:** Dactyls can be used to increase BoS.
As support columns increase in number, the need for dactyls decreases.

General requirements for stability (**Fig.** 2.3.**1**) illustrates that, for continuous standing, a relatively large base of support (BoS, grey surface) is required to compensate for a condition wherein all body mass is supported by a single leg. Although monopedal organisms do not exist *per se*, this stance is a common temporary state for many bird species during rest and sleep. However, the toes must be relatively long to provide a suitable BoS in respect to the single support column.

Two legs are better suited to a stable stance since the resulting BoS polygon is larger when compared to one-legged standing on comparably sized feet/toes. A further increase of stability can be achieved by placing the feet further apart by splaying the legs and/or widening the pelvis. In the latter case, the inter-acetabular distance increases to allow a wider stance (and larger resultant BoS) while maintaining the vertical column of support with the legs.

Fig. 2.3.**1** illustrates that – as limbs decrease in number – an organism compensates by increasing the area of its ground contact surface, i.e. foot, paw, toes. Conversely, an organism with a greater number of limbs can reduce the ground contact surface as commonly seen in hoofed quadrupeds. As illustrated, bipeds can also augment stability by placing the limbs further apart. Finally, short limbs reduce the risk of tilting while longer limbs compound this risk because a comparable displacement of the trunk, i.e. CoM, will shift the perpendicular (red vertical line) out of the BoS in the long-legged biped while remaining within acceptable boundaries in a short-legged organism.

Dynamics and strategies for efficient bipedal walking

Walking stride in humans is achieved when each foot contacts the ground for more than half of total stride time. This translates to a duty factor (df) exceeding 50% and does not include an aerial phase. In the portion of stride cycle where only one foot is on the ground, articular control is of utmost importance to maintain balance due to the constant movement of the trunk relative to ground. To maintain balance, the connecting hip joint between trunk and stance limb is a highly mobile ball-and-socket joint which, in humans, can compensate for out-of-balance conditions in all directions. In birds, the femur head is only partly inserted in the hip socket and thus exhibits a smaller motion range. This restraint is compensated by action at the knee which, as opposed to humans, can be lateromedially rotated during stance phase (e.g. Stolpe, 1932).

When walking, the human body (and consequently its CoM) is at its lowest point when the legs are furthest fore and aft during swing phase and CoM is at its highest point in mid-stride when a leg is grounded directly beneath the torso (e.g. Alexander, 2003; Vogel, 2003). Consequently, the CoM moves rapidly up and down at the extremes of the stride and almost not at all during mid-stride with gravitational and kinetic forces interchanging as in a pendulum. This out-of-phase relationship between gravitational and kinetic energy provides a continual impetus during walking. In a study including rheas and turkeys, Cavagna et al. (1977) showed that during intermediate walking speeds the resulting transfer of kinematic and gravitational energy accounts for more than 70% of entire energy transmission, leaving only 30% provided by musculature. At a certain point, gravity limits the frequency range over which a leg can be swung and the body raised and lowered – much like a given pendulum swings at a natural frequency. To increase speed, one will swing the legs farther in the fore/aft plane rather than more frequently. However, after reaching a particular amplitude, the gravity-limited arc of limb/pendulum motion prevents a further gain in velocity (e.g. Alexander, 2003; Vogel, 2003). Fast, efficient walking is achieved by balancing the optimised natural stride frequency with the maximally effective limb length (e.g. Preuschoft & Christian, 1999).

The combination of these factors is succinctly expressed by the principle of eigenfrequency, explored in more detail on the final page of this thesis. This wide-ranging concept is intrinsic to the achievement of optimised locomotor dynamics, wherein a wide range of variables – including bone density, limb segment length, distribution of muscle mass, overall body mass and metabolic parameters – are synergised to promote a harmonised oscillation among all elements to ensure dynamic equilibrium in movement. The achievement of this fluid relationship within the stride cycle minimises the overall demand for energy in steady locomotion. An organism can possess a range of strides, each reflecting a specific eigenfrequency, as clearly exemplified in humans by the highly efficient walking stride and an altered, but similarly energy-efficient long-endurance running gait.

While human beings exhibit a distinct transition when changing gait from walking to running (including obvious changes in duty factor and step length) this transition can hardly be detected when observing birds. Avian species gradually modulate from walking to a bouncy running gait with duty factors still above 0.5 (Gatesy & Biewener, 1991) and is identified as a very economic gait for intermediate speeds (Rubenson et al., 2004). This incremental gait transition is likely due to the difference in avian hind limb segment orientation and joint articulation when compared to humans. In general, smaller bird species have longer step lengths, excursion angles and duty factors due to a rather crouched posture when compared to larger birds (Abourachid & Renous, 2000; Gatesy & Biewener, 1991).

Dynamics and strategies for efficient bipedal running

To move faster and still derive residual energy from the inherent dynamics of a stride cycle, a person or animal will shift to a running gait. The CoM now moves in a rather straight line in relation to direction of travel and energy can no longer be recovered to the same extent by interchanges of gravitational and kinetic energies in the up/down direction (Alexander & Jayes, 1978). To compensate for this lost potential energy, running vertebrates store and release elastic energy in tendons where the degree of elastic energy storage generally depends on length, diameter and elastic properties of the tendons (e.g. Alexander, 1984 & 1988; Alexander & Bennet-Clark, 1977; McMahon & Cheng, 1990). Predictably, the elastic properties of most hind limb muscle tendons in the ostrich appear to be very pronounced (Alexander et al., 1979; Smith et al., 2006).

Overall, the power output of limb muscles in large animals like the ostrich seem to be relatively more effective than those of smaller species. This has been presented over a wide range of avian and mammalian subjects by Alexander, 2005. As a strategy for economic running at intermediate speeds (3.5 ms^{-1}), Rubenson et al. (2004) found that “the selection between an inverted-pendulum walking gait and grounded running in ostriches results in a minimisation of metabolic-energy costs of locomotion”. His study “significantly strengthens the argument that a minimisation of metabolic-energy costs is an important determinant of gait selection in terrestrial animals”.

As in walking, limb length influences stride length and is thus positively correlated in equations of maximum speed potential. Some animals increase stride length first while others increase stride frequency. Abourachid and Renous (2000) and Abourachid (2001) found that in order to increase speed, ostriches increase stride frequency first while the much smaller kiwi increases stride length. This results from the different limb axis alignment in smaller, lighter avian species which exhibit a flexed jointed chain system while larger, heavier cursorial birds possess an extended jointed chain system to maximise a gravity-induced system (Abourachid & Renous, 2000). In this context, it is important to introduce the principle of “effective limb length” where not only absolute length of the extremity is considered but also maximum joint protraction angles to derive the extent of the limb’s functional capabilities in locomotion (Gatesy & Biewener, 1991). Thus, birds with apparently 'short' legs, like quail, have been found to possess relatively greater effective limb length than the ostrich. However, with step lengths of up to four metres, the ostrich still exhibits greatest step length of any biped in absolute terms (Alexander et al., 1979).

Another important factor influencing running dynamics is the expression of ground reaction forces (GRF). During standing, GRF simply opposes the force the mass of a body exerts on the ground and acts exclusively in the vertical direction. With increasing speed, the GRF is compounded by horizontally vectored forces. Clark & Alexander (1975) found in their study of running quail that the work of muscle-tendon units increases due to these horizontal forces. However, these inertial forces also play an important role in the balance and support of the body/trunk, contributing to economised net muscle force (e.g. Chang & Kram, 1999).

To a great degree, maintenance of balance during running is provided by the principle of dynamic stability wherein the inertial mass of the animal provides momentum to the free-moving body, increasing the predictability and constancy of its inertial vector. This phenomenon allows efficient focus of muscle force towards propulsion, with energy diverted to balance management only when CoM and stability require correction, and is most beneficial during straight locomotion when transverse inertial forces are minimised. Cursorial species in particular will direct as much force as possible towards propulsion. This preference can be reflected in structural features of the joints, where “form closure” joints are highly guided by their inherent morphology and “force closure” joints require greater proportional muscle power to control and manage the range of motion (Bögelsack et al., 2000). Additional energy savings can be realised through morphological restrictions to degrees of freedom by the arrangement of passive structures like joint surface contours, protrusions and ligaments. This is particularly important for endurance locomotion where every structural attribute which does not directly consume metabolic energy combines to deliver a net energy benefit to the organism. A worthy example of divergence in abilities is provided by comparison between the cheetah and ostrich.

The cheetah is able to accelerate much faster and achieves higher maximum running speed (~ 110 kmh^{-1} *vs.* ~ 80 kmh^{-1}) but can only sustain these speeds for a very limited time span. However, the cheetah retains great manoeuvrability in its distal limb segments, coupled with appropriate muscular and neural control *via* force closure joints, and is able to execute instantaneous changes in direction at top speed as well as climb trees and grab prey. By comparison, the ostrich, with form closure joint anatomy, sacrificed this range of articulation to optimise its abilities towards speed and endurance. As a further illustration of this sliding relativistic scale, intra-species differences between endurance running and acceleration have been found (e.g. Crook et al., 2008; Weyand & Davis, 2005) among human and equine specimens wherein sprinting specialists possess relatively more muscle mass than endurance runners. This arrangement provides high short-term power output but negatively affects endurance performance. In general, sprinters may increase traction surface and/or appendices for greater grip (e.g. claws) while an endurance runner will reduce mass at the distal limb to minimise negative impact on the swinging capacity of the limb. When viewed in the context of fast and steady locomotion, extra mass in the distal limb results in an energetic disadvantage in accordance with the Law of the Pendulum. This principle states that the pendulum will swing slower as an applied mass is shifted away from the pendulum's pivot point, as conversely exemplified by the metronome's increased tempo as the weight is moved closer to the pivot point:

$t = 2\pi\sqrt{l/g}$ where t = period, l = length of the pendulum, g = gravitational acceleration.

These various principles are applied and explored throughout this study in respect to ostrich morphology and locomotion.

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3 Materials and methods

Methods employed in this study include comparative morphology and morphometry and analyses of kinematics, joint mechanics and pedobarography. A detailed description of each method, associated materials and set-ups is provided in the corresponding sections of each Results chapter.

3.1 Integrative approach

In this study, the focus is concentrated on structural attributes of the locomotor apparatus and its kinematic expression in the ostrich to determine the existence of specialisations that allow extreme locomotor performance. Methodological investigation of specific metabolic functions is planned for a subsequent study. Existing data are integrated into the overall scheme of ostrich locomotion when relevant (see **Fig.** 3.1.**1**).

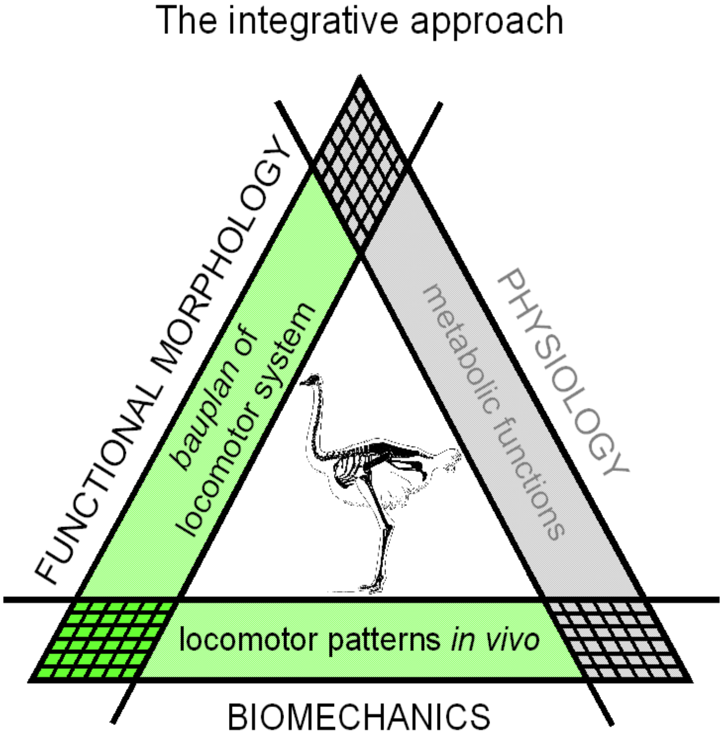

Fig. 3.1.**1**: Intersection of methods with green sections indicating the areas of inquiry.

3.1.1 Functional and comparative morphology

a) Dimensions of skeletal elements influence statics and dynamics of the hind limb

Insight into specialisation can be gained by morphometric comparisons among avian species. Skeletal morphometry is an important indicator of lifestyle and has been used to analyse the cursorial behaviour of avian species in combination with allometric studies (e.g. Abourachid & Renous, 2001; Alexander, 1983; Casinos & Cubo, 2001; Cubo & Casinos, 1994; 1997; Maloiy et al., 1979). In the present study, the functional lengths and relationships of the limb segments are analysed instead of maximum segment lengths as generally presented. Data of functional lengths has higher relevance in studies that incorporate biomechanics (Chapter 4.1.2 and 4.1.3).

b) Musculature serves simultaneously as an active power generator and passive structure *via* mass distribution and functional interconnections

Muscle mass distribution is an important factor in the swinging properties of the limb. Intraspecific differences have been found in *Homo sapiens* when comparing the distribution of crural muscle mass amongst sprinters and marathon runners (Weyand & Davis, 2005). As the crural muscle mass is shifted proximally towards the Centre of Mass, the moment of inertia of the entire limb is reduced and improves performance (e.g. Preuschoft & Christian, 1999).

Distal muscle mass can also be reduced to further improve swing dynamics. This study presents the muscle mass morphometry of two similar ratite species to identify optimisations towards long endurance locomotion in the ostrich (Chapter 4.1.2). The inclusion of functional morphology is crucial to an understanding of ostrich locomotion and dissections are performed to analyse limb construction and function (Chapter 4.1.1).

3.1.2 Biomechanics and locomotor dynamics

a) Passive structures of the locomotor system for stabilisation and management of motion without additional energy expenditure

Abourachid (2001) described the relationship between size and functional/morphological features in respect to adaptations for terrestrial locomotion in various avian species using a kinematic investigative framework.

The present study offers data on kinematics and joint anatomy with the hypothesis that *Struthio*'s disposition towards stability during slow locomotion and exceptional high-speed performance is augmented by anatomical conditions and structures that manage muscle-powered limb motion to maximise energy output efficiency during all stages of locomotion. Many of these structures operate on a “passive” basis as a result of their inherent morphology. In order to quantify the net effect of these constraints and identify consistencies in the range of limb motion, kinematic data of adult ostriches during walking and moderate-speed over-ground running is correlated with anatomical analysis of the intertarsal joint (Chapters 4.2.1 and 4.2.2; 4.3).

b) Analysis of toe function

As refined devices for controlled grasping, scratching, clawing, swimming etc., dactyls are employed for myriad uses among avian species. This wide variety of applications makes isolated study of these structures as pure locomotor elements challenging. In contrast, the ostrich is highly specialised in its locomotor *modus operandi* and exhibits extreme functional restrictions in its use of the toes.

The present study examines the vital interaction between the substrate and toes, including dynamic analysis *via* pedobarography, to integrate the elements of ground contact within the context of locomotion (Chapter 4.2.3).

3.1.3 Integration

The final step in this approach is the integration of all collected data to allow a more complete understanding of the role of individual elements within the functioning whole (Chapter 5).

3.2 Ostrich raising, keeping and training

In order to derive accurate results within the framework of the integrative approach, it was important to engineer a situation where ostriches were kept in a manner appropriate to the species and allow the handler unlimited access to healthy, unstressed subjects. Specimens had to be approachable and rather tame to ensure a successful course of experiments. This high level of contact between keeper and subjects would provide the dual benefit of a calm, natural environment for the animals and relative safety for the handler during experiments. Adult ostriches are capable of dangerous kicks and can be aggressive to invaders of their territory (oral communication J. Gass), raising the potential for serious injury to either party. To achieve an acceptable level of safety and interaction, hand-raising the ostriches from a young age was considered the best solution. Crucial information about specimen origin would be obtained and monitoring of health and nutrition could be efficiently maintained. Months prior to receiving the young birds, information about appropriate ostrich raising and keeping techniques was gathered from ostrich farmers and a wealth of literature was used for reference to ensure a successful outcome (Brinkmann & Haefelfinger, 1954; Deeming, 1999; Faust & Faust, 1962; Huchzermeyer, 2002; Kistner & Reiner, 2002; Kreibich & Sommer, 1994; Krumbiegel, 1966; Nolte, 1895; Romer, 1997; Ruempler, 1978; Weinland, 1860).

The above criteria excluded farm and zoo specimens for a number of reasons. In general, farm specimens are slaughtered after reaching an age of 12 – 14 months and are considered sub-adult. To ensure accurate and meaningful results, only full-grown birds were used in these experiments. Zoo animals are often kept in inter-species enclosures and are rarely approachable. Furthermore, observations of zoo ostriches also revealed a typical degradation of the elevated metatarsophalangeal joint presumably due to insufficient exercise and lack of space for running. An experimental set-up in a zoo would likely conflict with zoo schedules and preclude modification to the enclosure as required by certain experiments.

Perhaps the greatest benefit of constant interaction between the author/keeper and subjects over a period of years was the rare opportunity to engage in very close observation of these birds to gain an intimate understanding of their behaviours, postures and locomotion patterns. The data presented in this work was not collected using caged or stressed animals or derived from experiments with treadmills that can, in some circumstances, yield misleading results (Rubenson et al., 2007). Finally, the birds used in this study will not be euthanized but will instead enjoy an untroubled life until their natural death.

Fig. 3.2.**1**: Dimensions of enclosure

Fig. 3.2.**2**: Ostrich chicks after arrival

Fig. 3.2.**3**: Ostrich Tiffy in July 2007

3.2.1 Raising

Three 10-week old female ostrich chicks were received in September 2004 from a local breeder in Germany (**Fig.** 3.2.**2**). Over the first six months, the keeper's daily presence within the enclosure habituated the birds to human contact. As three fully-grown ostriches already inhabited the enclosure, the behaviour of all birds had to be monitored closely to prevent possible attacks on the ostrich chicks by the stronger dominant adults. Fortunately, the familiarisation period progressed without incident and the chicks were accepted into the group. For the first year, the young birds were fed a special ostrich chick diet on a daily basis. Subsequently, all ostriches were fed a special mix of seeds and grains daily in wintertime and every second day during the vegetation period when pasturage is widely available within the enclosure. During the first two winters (October to March), the growing ostriches were kept in a weatherproof barn at night to protect them from inclement weather conditions. Fresh water was freely accessible to all birds.

3.2.2 Keeping

The enclosure is located in a hilly area within a nature reserve (Odenwald, Southwestern Germany) measuring 6400 m^2 (**Fig.** 3.2.**1**) comprised of grassy pasture. It contains one major barn with a specific foil sheet membrane where the birds are fed and protected from the elements. Three smaller solid wooden shelters provided additional wind/rain protection within the enclosure. Floor surfaces in the shelters are covered with straw and replaced periodically to ensure a dry and clean environment. A large sandpit, also periodically refilled, ensures that the ostriches can take daily sand baths to maintain healthy plumage and skin. These housing conditions meet or exceed German laws for ostrich keeping. All animal experiments were officially licensed and registered. A major challenge occurred in autumn 2006 when, as a consequence of cases of avian influenza (H5N1 virus) in Germany, a general order to keep all 'poultry' inside housing systems essentially prevented outdoor experiments for a period of time.

3.2.3 Training

To collect significant data from the kinematic and pedobarographic experiments, it was crucial that the ostriches would perform without being physically directed or adversely influenced in any manner. By the time these experiments were carried out, animals were accustomed to human contact (**Fig.** 3.2.**3**) and habituated to certain vocal signals learned during training. In order to establish comfort and safety for subjects and handler while walking and running in the on-site corridor (detailed set-up described in Chapter 4.2.1, 4.2.2 and 4.2.3), the birds were allowed free access to the experiment site within their enclosure eight weeks in advance of data gathering. Since the corridor was divided from the main enclosure only by meshed wire, the individuals could maintain eye and acoustic contact with their flock to eliminate stress levels. During the weeks of set-up habituation, the handler walked and ran alongside the birds with the result that the birds mimicked this behaviour. Rewards of extra food portions were offered as incentive at the end of successful trials. After four weeks, a mocked-up pressure plate was positioned on the ground in the corridor. As expected based on previous observations, the animals reacted in a suspicious manner to the new device and avoided stepping on it. By placing food on the plate and with the handler demonstratively standing on the mock-up, the initial rejection disappeared. After a few more days, the ostriches chose to step on the plate deliberately.

3.3 Itemisation of methods

The following scheme (**Fig.** 3.3.**1**) depicts the chronological sequence of all analyses, experiments and concurrently employed methods over the course of this project.

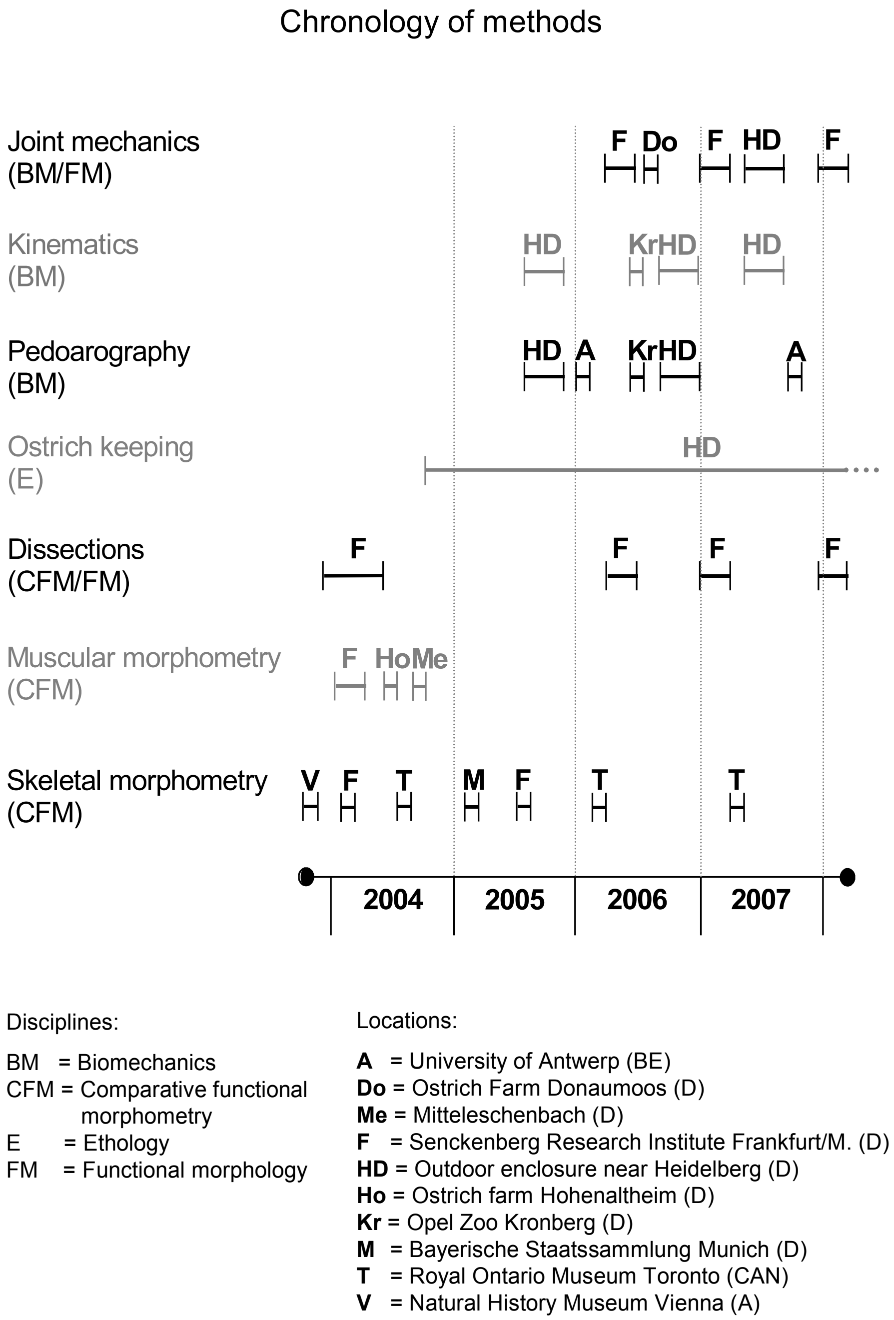

Fig. 3.3.**1**: The chronology of methods depicts the concurrent nature of multiple disciplines.

As illustrated, the approach for this study included a 'rotating system of methods', with dissections, observations, kinematic analyses and pedobarographic methodologies used, reviewed or revisited whenever relevant, constantly augmented by research into the work of others in the field. This system of inquiry delivers many advantages due to its malleable structure, offering intensive periods of experimentation followed by digestion of information and periodic reformatting of approach as new information or viewpoints emerge. This facilitates recombining methodologies and refocusing goals, ultimately providing a high level of understanding of the interplay of ostrich subsystems and forming the essential framework for defining the '*Funktionsmodell*' or integration as proposed by Herkner (1999). For example, if an unexpected locomotor behaviour occurred during observations, a morphological analysis could be undertaken to determine the relevance of this behaviour. Those results may further narrow the focus to subsequent kinematic analysis of a particular trait. Although this approach may diverge somewhat from conventional current-day practises, it was of incalculable value in assembling this body of work. In summary, this experience has revealed that any scientific inquiry is also constantly evolving, where no process of inquiry can be declared 'finished' and subsequently abandoned. Instead, this scientific inquiry should be viewed as an 'open-ended' study.

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4 Results and analysis of locomotor system

4.1 Functional and comparative morphology

In the following three Results chapters, morphological and morphometric analyses are employed to determine the underlying structures in the locomotor apparatus of the ostrich. In the subsequent three chapters, derived morphological information is integrated with dynamic analysis of ostrich locomotor patterns.

4.1.1 Morphology

As the underlying physical basis for this integrative study, a thorough understanding of muscle locations and interrelationship within *Struthio*'s hind limb is required to facilitate interpretation of locomotor function. The descriptive and functional morphology of the pelvic limb of the ostrich and its ratite relatives has long received particular interest due to their status as flightless, highly cursorial avian species (e.g. Gadow, 1880; Gangl, 2001; Gangl et al., 2004; Garrod & Darwin, 1872; Haughton, 1865; Liswaniso, 1996; MacAlister, 1865; Mellet, 1985; Patak & Baldwin, 1993 & 1998; Pavaux & Lignereux, 1995). General information about ratite hind limb musculature can be obtained in Bezuidenhout (1999), George & Berger (1966), Raikow (1985), van den Berge & Zweers (1993) and others. Additionally, the food industry provides cutting schemes for pelvic muscles of the ostrich which are used to determine qualities and quantities of specific muscles.

General functional interpretation of a certain muscle can be presented on different levels. Description of areas of origin and insertion, as well as the course of a specific muscle/tendon, allows basic predictions about resulting effects on the motion range of the skeletal elements and joints through which it is connected. To a certain degree, these predictions can be supplemented by observations of *in vivo* locomotor patterns. Stolpe (1932) termed the combined study of live and anatomical subjects “physiological anatomy”. This methodology also takes into account that an extremity may have multiple uses, employed in various modes of locomotion in addition to display, grooming, defence or thermoregulation.

The characteristics of a muscle can be further specified by investigating its structural architecture, including classification as ordinary or pinnate, analyses of the ratio of slow and fast fibres and determination of sarcomere length and diameter (e.g. Alexander & Ker, 1990; Gans & Bock, 1965; Rome, 1992). These data reveal whether a muscle delivers fast and strong but short-term power output as required for fast acceleration manoeuvres or whether it is operating at a slower rate, thus enabling steady locomotion (Vogel, 2003). As a consequence of each species’ particular locomotor pattern, various intermediate stages of muscle composition can be expected. Detailed data about pinnation angles, fascile lengths and volume and histochemical data of ostrich hind limb muscles is presented *inter alia* by Mellet (1985), Sales (1996) Velotto & Crasto (2004), Viljoen et al. (2003) with additional data about maximum power output and tendon properties reported by Smith et al. (2006). Data on fibre lengths have been incorporated with body and muscle masses and muscle moment arms to derive species-specific allometric equations which allow conclusions about motor patterns over a wide range of animals, including cursorial birds (e.g. Alexander et al., 1981; Bennett, 1996). Another important quality found in musculature is the ability to store and reflect elastic energy within the connective tissue and in myofibrils *via* the protein titin (e.g. Opitz et al., 2003).

In this primary level of investigation, existing ostrich-specific morphological data and functional interpretations are integrated with dissections and observation of live ostriches. Despite the wealth of available data, it is indispensable to carry out dissections to gain first-hand insight into ratite morphology as a baseline for subsequent inclusive research about the ostrich. Furthermore, certain authors still disagree on a range of specifics including the expression, or even the very existence, of certain muscles (e.g. Gangl, 2001).

Within the framework of this integrative approach, the interspecific comparison of related species is highly suited to the definition of species-specific peculiarities. Towards this end, a close relative of the ostrich, the lesser rhea (*Pterocnemia pennata*), has been selected for comparative morphological examination.

Material and methods

Two formalin preserved lesser rheas (adult male and female) and two fresh ostrich specimens (two adult females stored at 4 °C) were macroscopically dissected. The muscles were removed gradually and, in the case of the female rhea, each dissection step was photographically recorded, rendering a total of 261 photographs. The complete dissection of one ostrich hind limb was documented with two video cameras both situated at a 4 m distance from the specimen at a 90° angle to capture lateral and front view simultaneously (Canon 900 & Canon 500i, 25 fps). Concomitantly, a detailed dissection report was formulated, including drawings. Subsequently, detailed schemes of the ostrich hind limb were drawn depicting all muscle layers from the lateral and medial perspective.

Additional investigations included:

- Observation and video recording of various modes of locomotion (level, in- and declined walking and running, resting, sitting, scratching) of ostriches and lesser rheas (Opel Zoo, Kronberg).
- Skeletal analysis of large ratites in ornithological collections

The functional interpretations of muscle function have been obtained by Fuss (1996), i.e. F, Gadow (1880), i.e. G (1880), George & Berger (1966), i.e. G & B, Haughton (1865), i.e. H, Mellet (1985), i.e. M, Raikow (1985), i.e. R, Stolpe (1932), i.e. S, van den Berge & Zweers (1993), i.e. VB & Z.

Results and discussion

Specific differences in muscular morphology between ostrich and lesser rhea

Detailed topography of ostrich hind limb musculature can be obtained from various sources (e.g. Bezuidenhout, 1999; Gangl, 2001; Gangl et al., 2004; Liswaniso, 1996; Mellet, 1985; Pavaux & Lignereux, 1995). Topography of hind limb musculature of the lesser rhea is presented as schematic drawings and pictures in the appendix **Table apx 1-3.**

In the lesser rhea, the M. iliotrochantericus medialis, not found in the ostrich, originates at the preactebulum and inserts laterally at the Trochanter femoris to effect femoral adduction. In both ratites the M. pectineus originates at preacetabular ilium but, in the rhea, is also connected to the last dorsal vertebrum (rib) and at the pectineal process. Since the femur is relatively longer in Rheidae than in Struthionidae (Chapter 4.1.2), the increase in lever arm forces require additional insertion areas to support muscle power in the management of hip flexion.

Features of the lesser rhea that differ from the ostrich include:
i) the M. ambiens does not connect to the toe flexors but instead inserts in the tendofascial sheet of the knee.
ii) the M. femorotibialis possesses no accesorius.
iii) the M. gastrocnemius possesses a fourth component, the pars supramedialis.

Perhaps the greatest morphological difference is evident in the toes. Since the lesser rhea possesses a fully developed 2nd toe, it also features all related musculature to activate and control this digit. In concert with a complete reduction of the inner 2nd toe, the ostrich has reduced the M. flexor perforatus digiti II and M. extensor brevis digiti II. In skeletal specimens, only a vestigial remnant is still present at the distomedial trochanter (own observations).

Functional interpretations of the pelvic limb musculature of ostrich

The nomenclature is based on the Nomina Anatomica Avium (Baumel, 1993). A detailed list of obsolete nomenclature can be found in Gangl (2001). **Table** 4.1.1.**1** lists all muscles with corresponding interpretations according to the existing literature. Generally, all muscle locations are in accordance with Gangl (2001) and Gangl et al. (2004). As opposed to George & Berger (1966), only two iliotrachanterici were found in the ostrich.

Stolpe (1932) noted that all muscles responsible for rotation are weakly developed with the exception of the M. obturator. This is in agreement with the hypothesis that the mediolateral rotation is typically limited in cursorial species (e.g. Hildebrand, 1988) with joint excursion rather focussed towards fore-aft motion (Chapter 4.2.1).

Generally, distally originating muscles (distal femur to toes) are biarticular. Elements of pelvic musculature and/or muscles responsible for internal/external articular rotation are generally not biarticular. In a related study, Ellerby and Marsh (2006) concluded that “the low energetic cost of carrying trunk loads in guinea fowl may rely on the activation of a group of biarticular muscles that together provide support and propulsion across all the major joints, without producing opposing moments at other joints that could potentially waste energy.” This observation reflects the identification of physical attributes relevant to this study and indeed, the ostrich possesses many bi- and triarticular muscles (indicated in **Table** 4.1.1.**1**). These muscles connect knee, intertarsal joint, metatarsophalangeal joint and toes to coordinate motion of the distal limb within a system that features a high degree of coupled motion. Conversely, the proximal muscles provide hip stabilisation and act directly on the knee as the joint of major limb orientation adjustment, with function similar to the human hip joint with its relatively wider range of motion when compared to distal joints.

In agreement with most existing literature, it has been found that certain muscles and corresponding tendons are not only biarticular but are also interconnected *via* shared areas of origin and insertion establishing functionally multi-jointed systems. It can be assumed that these interconnections are very important for automated/coupled limb movement possibly resulting in balanced additive and subtractive forces. To-date, quantifying these effects has not been adequately accomplished using mechanical models, much less in live systems. Experiments in subsequent chapters include comparison of morphological knowledge yielded from anatomical specimens with live kinematics and might reflect the effects of these coupled muscle-tendon systems in the ostrich (Chapter 4.2.1 – 4.2.3).

Contrasts in environment and habitat appear to be reflected in certain morphological differences between lesser rhea and ostrich. The lesser rhea lives in the uneven terrain of the Andes and can be found in altitudes up to 4500 metres. These variations in habitat are reflected in obvious differences in phalangeal design in the lesser rhea, specifically evident in the prominent claws on each of the three toes delivering increased grip on rocky substrate and a larger relative BoS. This would facilitate a greater degree of control for in-/decline running in this smaller ratite (max. 25 kg). Like ostriches, lesser rheas can run as fast as 60 km/h but, unlike ostriches, are unable to maintain these speeds and instead employ zigzag manoeuvres and short bursts of speed to escape predators (Del Hoyo et al., 1992) with these abilities supported by the morphological specialisations itemised above.

A common quality in all cursorial species, both bipedal and quadrupedal, is a shift of limb muscles towards the trunk and hip joint with actuation of the elongated distal limb elements *via* long tendons to decrease mass in the swinging part of the leg (e.g. Hildebrand, 1988). This typical mass relocation strategy is clearly evident in the ostrich which, as a specialised endurance runner, has proximally concentrated its muscle mass to a greater extent than seen in similar species. In addition, several long tendons connect proximal tibiotarsus to toes (see **Table** 4.1.1.**1**). Supporting data is presented in Chapter 4.1.2.

In addition to muscle mass distribution, the composition of muscles might further influence cursorial performance. Liu & Nigg (2000) incorporated the effect of 'wobbling masses' in a model of mass distribution in human runners and found that a reduced wobble effect resulted in better running performance. In this context, it is important to note that ostrich pelvic muscles contain the lowest fat content in comparison to other birds, including the other ratites (Deeming, 1999). The influence of wobble mass on speed and energy consumption may be negligible for short locomotor events but would have a more significant effect during episodes of steady running where a multiplicity of lesser factors converge to affect overall performance and energy requirements.

Interconnected muscle-tendon systems and possible benefits in ostrich locomotion

The interconnection of the femur adductor M. pectineus with the hip flexor/knee extensor M. iliotibialis cranialis and knee extensor M. femorotibialis (see **Table** 4.1.1.**1**) may be useful during the final portion of swing phase. Shortly before touch-down in moderate-speed running, the ostrich femur is slightly adducted, with the hip flexed and knee extended (Rubenson et al., 2007). This implies that all three muscles could be working as a functional unity in accordance with the principles of a coupled/automated chain of motion. However, this does not suggest that muscles which are interconnected through shared areas of origin and insertion, or which are actually connected *via* fascia (as M. pectineus and parts of M. iliotibialis cranialis), are unable to work independently.

The Tendo lateralis of the M. fibularis longus, acting as a strong intertarsal joint extensor inserts between the endtendon of the M. gastrocnemius – also a strong intertarsal joint extensor – and finally merges with the tendon of the M. flexor perforatus digiti III. The Tendo caudalis of the M. fibularis longus inserts into the Cartilago tibialis which provides a channel for the majority of the toe flexor tendons. In the live ostrich, the intertarsal joint is fully extended only during stance phase (e.g. Rubenson et al., 2007; Chapter 4.2.2, intertarsal joint). Simultaneously, the toes are slightly flexed to increase grip and stability on the substrate (Chapter 4.2.3, dynamic toe function).

The highly synchronised interplay of these muscle-tendon systems could be argued to provide a locomotor assist strategy above and beyond the application of pure muscle power. The significance of this system is apparent when considering that it is primarily active throughout the time of maximum trunk load on the pelvic limb in stance phase.

As indicated in **Table** 4.1.1.**1**, the M. ambiens is connected to strong toe flexors thus forming a muscle-tendon complex which runs over all four limb joints while crossing from medial (as M. ambiens at femur) to lateral side (M. flexor perforatus digiti III at proximal tibiotarsus and from intertarsal joint resuming cranially to the plantar surface of the 3rd toe). This orientation may be of importance for economic toe flexion at push-off when the knee is simultaneously extended (Brauer, 1911; Gatesy & Biewener, 1991; Rubenson et al., 2007).

Elongated Crista cnemialis cranialis for optimised lever capacities of involved muscle-tendon systems

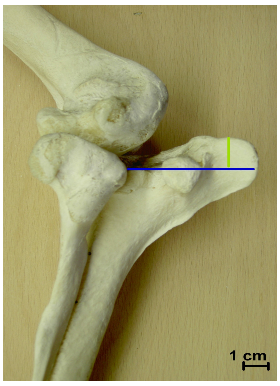

Fig. 4.1.1.**1a**: Crista cn. cr. of adult ostrich.

To increase muscle power output, muscles are often arranged to act over protrusions located near the joint's centre of rotation like, for example, the human M. gastrocnemius at the ankle/talocalcanean joint at the heel (Alexander & Dimery, 1985; Vogel, 2003). Optimised muscle power transmission incorporating a protruding lever is an important component of a cursorial species effort to sustain long stride length and high swing frequency. These two goals are essentially achieved by an effective limb length and appropriate muscle power output to drive the limb through swing phase. Fowler (1991) has proposed that the structural protrusion or "jib" provided by the Crista cnemialis of the proximocranial tibiotarsus allows the involved musculature to increase leverage force in the ostrich limb. A similar advantage, but to a lesser degree, could be attributed to the lever-like protrusion of the caudally elongated hypotarsus at the proximal tarsometatarsus. As opposed to many bird species, the Crista cnemialis is well developed and cranially elongated in the large cursorial ratites (**Fig.** 4.1.1.**1a**, right knee, lateral view). The shape and orientation of the Crista cnemialis cranialis indicates particularly advantageous leverage capacities among knee extensors and flexors of the intertarsal joint in the ostrich. Muscle origins and insertions at the tibiotarsal Crista cnemialis are documented herein, including explanations for morphological differences in this protrusion between rhea and ostrich.

In accordance with Gangl (2001) & Gangl et al. (2004) the following muscles have been found to be associated with the Crista cnemialis cranialis.

Muscles inserting at Crista cnemialis cranialis:	
M. iliotibialis cranialis	(hip flexor & knee extensor)
M. femorotibialis externus et accesorius	(knee extensor)
Muscles originating at Crista cnemialis cranialis:	
M. gastrocnemius Pars medialis	(intertarsal joint extensor and toe flexor)
M. fibularis longus	(intertarsal joint extensor and toe flexor)
M. tibialis cranialis	(intertarsal joint flexor)
M. extensor digitorum longus	(toe extensor)

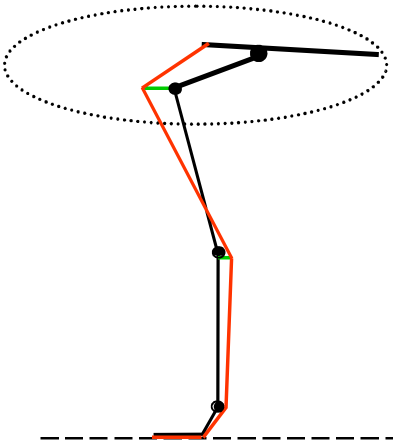

Fig. 4.1.1.**1b**: Schematic of interconnected muscle-tendon system over the levers of Crista cnemialis and Hypotarsus.

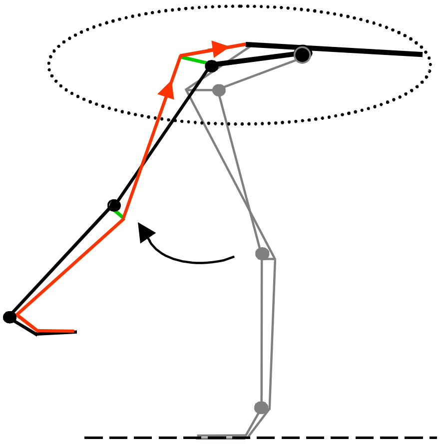

Fig. 4.1.1.**1c**: Proximal tractive impulse through lever system in limb protraction.

Two significant knee extensors – the Mm. iliotibialis and femorotibialis – insert directly at the Crista cnemialis cranialis. The ostrich knee is extended twice in the stride cycle, both during the second half of the swing phase (see **Fig.** 4.1.1.**1b** + **c**) and at push-off with higher excursion angles at running speeds, indicating the vital role of this joint and its interconnecting structures in locomotor performance (e.g. Stolpe, 1932; Chapter 4.2.1). It is important to note that the existing literature places emphasis largely on retraction of the limb where powerful push-off/dynamic impulses accelerate the body in the direction of locomotion (e.g. Seyfarth et al., 2003). Limb protraction receives significantly less attention despite the often-overlooked fact that it is energetically expensive. Not surprisingly, it has been found in guinea fowl that it is more costly to swing the limb than previously estimated (Ellerby & Marsh, 2006). But this is only part of the story: It must be kept in mind that during a full stride cycle in high-speed running, the swinging limb is arrested at the end of the stride and, after push-off, must be re-accelerated *via* protraction to the point where it overtakes the body in preparation for touch down. As can be appreciated, this is quite an achievement at speeds exceeding 50 kmh^{-1}. This period in the stride cycle is crucial to overall speed, wherein effective protraction has a direct correlation to maximisation of step length, and speed of protraction has a direct correlation to stride frequency. For the large heavy ostriches, emus and rheas, minimising the metabolic cost of limb swinging is an obvious benefit towards efficient locomotion with the Crista cnemialis providing a prominent structural attribute towards improved power transmission. In this context, it would be very interesting to measure the actual power output of all muscles associated with the Crista cnemialis in running ostriches following the method of Ellerby et al. (2005).

While the Crista cnemialis is quite similar in all large ratites, its orientation differs inter-specifically. In the ostrich it is oriented cranially while in the lesser rhea it is slightly medially oriented. This difference may arise from the slightly different limb segment dimensions (Chapter 4.1.2) and limb postures (Chapter 4.1.3) that result in tuned traction and leveraging capacities *via* the involved musculature as required for variations in habitat.

Table 4.1.1.**1:** Function of ostrich hind limb muscles

A. PELVIC MUSCLES	**INSERTION**	**References**	**Articu-lation**	**Additional remarks and interconnections**
		1. Hip flexion & femur rotation; Originating at preacetabular & acetabular ilium		
M. iliotrochantericus caudalis	Distolateral Trochanter femoris	Medial rotation & adduction of femur (G; M)	**direct**	
M. iliotrochantericus cranialis	Lateral Trochanter femoris	Craniomedial rotation of femur (G; M)	**direct**	
M. iliofemoralis externus (parted in 2)	Crus craniale laterally of Trochanter femoris, Crus caudale distally of Crus craniale	Rotation of Os femoris in acetabulum (M); Part 1 flexes hip/lifts & rotates femur medially, part 2 sustains femoral position with slight abduction (G)	**direct**	The M. pectineus, the most medial of all pelvic muscles (Gangl, 2001) does not insert at Proc. pectinealis as in other ratites incl. lesser rhea (own observations). A large portion of it is <u>connected</u> to the M. femorotibialis internus and shares insertion areas with this muscle and the M. iliotibialis cranialis. As in Gangl (2001) the medial fascia of the M. iliotibialis cranialis is fused with a fascial layer of the Pars medialis m. gastrocnemius (extensor of the intertarsal joint).
M. iliofemoralis internus	Proxial femur	Slight medial femur rotation (M); Slight hip flexion & lateral femur rotation (G)	**direct**	
M. iliotibialis cranialis	Crista cnemialis cranialis, knee aponeurosis & Extremitas proximalis tibiotarsi	Hip flexion & knee extension (G; M)	**direct**	
M. pectineus	Osseus fossa at Extremitas proximalis tibiotarsi	Femur adduction (M; G)	**biarticular**	
		2a. Hip extension &/or lateral femur rotation; Originating at postacetabular ilium		
M. obturatorius lateralis (P. dorsalis et ventralis)	Via two crura at Trochanter femoris	Strong femur rotation (S)	**direct**	Generally, the lateral rotation of the femur leads to medial rotation of the tibiotarsus, reflecting the typical standing posture of ostriches.
M. obturatorius medialis	Proximolateral Trochenter femoris	Caudolateral femur rotation (M)	**direct**	
M. ischiofemoralis	Laterodistal Tr. fem.	Lateral femur rotation (M)	**direct**	
M. caudofemoralis (P. caudalis et pelvica)	Caudiomedially at proximal femur	Hip extension and femur abduction, tail control (G)	**direct**	
M. pubo-ischio-femoralis (P. lateralis et medialis)	Mediodistally at caudal surface of femur	Femur adduction (M), hip extension (S)	**direct**	

		References	**Articu-lation**	**Additional remarks and interconnections**
A. PELVIC MUSCLES	**INSERTION**			
		2b. Hip extension &/or knee flexion; Originating at postacetabular ilium		
M. flexor cruris lateralis	Dorsocranially at distal femur at fascial sheet	Hip extension & knee flexion (M)	**biarticular** (S)	Insertion area, i.e. fascial sheet is shared with tendinous origin of Pars supramedials m. gastrocnemius. Endtendons of M. flexor cruris lateralis and medialis insert close to endtendon of M. pubo-ischio-femoralis and origin of Pars intermedia m. gastrocnemius.
M. flexor cruris medialis	As M. fl. cr. lateralis but seperately from it	Knee flexion & antagonist to knee extension during contraction of other knee extensors (M)	**biarticular** (S)	
M. iliofibularis	Proximal fibula	Strong knee flexor (M)	**biarticular** (S)	
		2c. Hip & knee extension; Originating at postacetabular ilium		
M. iliotibialis lateralis (P. preacetabularis, inter-media, postacetabularis)	Condylus lateralis femoris	Hip- and knee extension with simultaneous abduction and lateral tibiotarsal rotation (G; M)	**biarticular**	As in Gangl (2001), the end-aponeurosis of this muscle interconects with M. femorotibialis medius and the Pars medialis m. gastrocnemius originates at its endaponeurosis.
M. ambiens	Proximolateral at Tuberculum m. iliofibularis	Knee extension (M)	**biarticular**	In the ostrich, the M. ambiens originates at the Ala praeacetabularis and not as in most birds at the Tuberculum praeacetabularis. This muscel runs distally along the medial side of the femur to the knee where its tendon crosses the patella and serves at the procimocranial tibiotarsus as the area of origin for the M. flexor perforatus digiti III. This interconnection may result in coupled muscle power transmission from pelvis to toes. The M. ambiens also rotates the knee.
B. FEMORAL MUSCLES				
M. femorotibialis externus, medius, internus et accesorius	Proximomedial Extremitas proximalis tibiotarsi	Knee extension (G; M)	**direct**	At area of insertion (Condylus lateralis femoris), M. f. externus is connected to tendon of origin of M. flexor perforatus digiti III

		References	**Articu-lation**	**Additional remarks and interconnections**
C. TIBIOTARSAL MUSCLES				
1a. Intertarsal joint extension & toe flexion; Originating at distal femur and proximocranial tibiotarsus				
M. gastrocnemius, P. lateralis, intermedia et medialis	Crista hypotarsi & prox. tarsometatarsus	Intertarsal joint extension and toe flexion (G, M)	**biarticular**	The fascial sheet which connects end tendon of M. gastrocnemius to tarsometatarsus covers the Tendo lateralis od M. fibularis longus, another intertarsal joint extensor. For additional connections see above.
M. fibularis longus	Tendo lateralis at prox. third of Tmt, Tendo caudalis at prox. Cartilago tibialis	Tendo lateralis extends IT joint, Tendo caudalis flexes toes (G)	**biarticular**	Specifically, the Tendo lateralis inserts fan-shaped on the tendon of the M. flexor perforatus digiti III (Gangl et al., 2004).
1b. Passive guidance of intertarsal joint motion; Originating at tibiotarsus distally of end of fibula				
M. fibularis brevis	Proximomedial Tmt		**direct**	Acts as intertarsal joint ligament (reduced to a tendon; see Chapter 4.2.2)
2. Toe flexion; Originating at distal femur and proximal tibiotarsus				
M. flexor perforans et perforatus digiti III (two crurae)	With two crurae medio- & lateroproximal at Lig. plantare of central interphalangeal joint		**tri-articular**	All of these muscles are interconnected and flex the entire toes as well as the individual phalanx. In context of the locomoting ostrich: shortly befor toe-off, M. gastrocnemius and fibularis fully extend the intertarsal joint while the toes flex in order to achieve powerful push-off.
M. flexor perforatus digiti III (two crurae)	Lateromedially at Phalanx I & prox. interphalangeal joint		**tri-articular**	
M. flexor perforatus digiti IV (three crurae)	Phalanx I-III at 4th toe		**tri-articular**	4th toe fine adjustment (see Chapter 4.2.3)
M. flexor hallucis longus	Phalanx ungualis of toe IV		**tri-articular**	
M. flexor digitorum longus	Phalanx ungualis of toe III and IV			

		References	Articu- lation	Additional remarks and interconnections
C. TIBIOTARSAL MUSCLES	**INSERTION**			
3. Intertarsal joint flexion, toe extension; Originating at Caput femorale (femur) and Crista cnemialis (tibiotarsus)				
M. tibialis cranialis (two crurae)	Tuberositas m. tibialis cranialis at Tmt	Intertarsal joint flexion (G)	**biarticular**	Proximity of insertion with M. extensor proprius digiti III and M. extensor digitorum longus; M. extensor proprius digiti III originates between forked endtendons.
M. extensor digitorum longus	4th & 5th phalanx of toe IV & 1st to 3rd phalanx of toe III	Toe extension (G)	**tri-articular**	
4. Fibula *vs.* tibiotarsus adjustment; Originating at proximal fibula				
M. popliteus	Proximocaudal tibiotarsus	Medial rotation of tibiotarsus (Fuss) & rotation of fibula around Tib. (Haughton)	**direct**	
D. TARSOMETATARSAL MUSCLES				
1. Toe extensors; Originating at proximal tarsometatarsus				
M. extensor proprius digiti III	Tuberculum extensorium of Phalanx ungulis (claw)	In ratites & tinamous regularly present but irregularly & rarely present in most avian species (VB & Z); More prominent in tree birds, less muscle volume but connection to M. tibialis cranialis in cursorial species (G&B)	**biarticular**	
M. extensor brevis digiti III	Proximally at Phalanx I		**biarticular**	
M. extensor brevis digiti IV	Medially at Phalanx I		**biarticular**	4th toe fine adjustment (see Chapter 4.2.3)
2. Toe abduction & flexion; Originating at proximal tarsometatarsus				
M. abductor digiti IV	Phalanx I	Abduction & slight flexion of toe IV (G, G & D)	**biarticular**	4th toe fine adjustment (see Chapter 4.2.3)
M. lumbricalis (two crurae)	At Ligamenta plantaria of metatarsophalangeal joints of toe III & IV	Indirect plantar flexion at base of Phalanx I of toe III (G); Fine adjustment of tendon of M. flex. dig. Longus (R)	**direct**	

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4.1.2 Morphometry

In the last two decades, the large ratites have received increased attention from diverse disciplines. While the ostrich farming industry promotes this animal for its healthy meat and high quality leather (Deeming, 1999; Kistner & Reiner, 2002), paleontologists investigating theropods as the terrestrial ancestors of all extant birds (Padian, 1998; Hutchinson, 2001, 2002, & 2004) look to the ostrich as a living link to the past. The ostrich, being the biggest and heaviest living bird, is able to "travel" at an average speed of 60 km/h for up to half an hour, making it the fastest steady runner (Alexander *et al.*, 1979; Del Hoyo *et al.*, 1992; Hallam, 1992). To achieve this unique form of near-continuous locomotional power, specific conditions of physical constitution (i.e. "mechanical" design), and metabolic efficacy must be exploited. All subsystems of *Struthio* must be effectively linked to achieve this locomotional capacity; it would be insufficient if just the locomotor apparatus was specialised for fast running. To feed the energy requirements of this endurance runner, the organism needs an efficient ventilatory system for high oxygen intake coupled with a powerful heart and circulatory system, the ability to process distinct food sources of suitable composition and energy yield rate, and optimised blood chemistry and supply.

Furthermore, heat conduction systems are required to balance the effects of metabolic work. Significant research has already been done concerning the morphology of the ostrich (Gadow, 1880; Firbas & Zweymüller, 1971; Schmidt-Nielsen, 1971; Vanden Berge & Zweers, 1993; Pavaux & Lignereux, 1995; Bezuidenhout, 1999; Gangl, 2001; Maina & Nathaniel, 2001; Wagner, 2004). With the advent of modern techniques, it has become easier to measure the metabolism of larger animals such as ratites (Crawford & Schmidt-Nielsen, 1967; Withers, 1983; Maloney & Dawson, 1994, Fuller et al., 2003) while advanced kinematic studies have explored rates of energy turnover during exercise (Fedak & Seeherman, 1979; Gatesy & Biewener, 1991; Roberts et al., 1998). Although there is a significant body of data containing many aspects of the above-mentioned disciplines, there has not been a concerted effort to regard the ostrich as an integrated system. This study seeks to investigate the discrete systems of *Struthio*, distil the pre-existing data pool and integrate the relevant findings within a holistic framework to determine key features and identify the metamorphic optimisations specific to this organism.

Materials and methods

Morphometric analysis of the pelvic and hind limb skeleton

The functional lengths of the ilium, femur, tibiotarsus, tarsometatarsus, and third toe of six ratite and five non-passerine bird species skeletons were determined. For the purposes of this study, functional length is defined as the distance from the proximal to the distal joint surfaces of each bone and disregards appendices such as cristae and processi, which protrude and therefore exaggerate the bone measurement. Among the digits, the third toe is considered the most significant due to its increased length (relative to other toes) and its primary role as a lever for balance, exertion of traction forces and directional impetus during locomotion. The third toe was measured from the tuberculum extensorium of the phalanx proximalis to the tip of the claw. Bone length data was included only if the skeleton was complete, undamaged and originated from an adult animal. Whenever possible, the skeletons of wild birds were investigated and skeletons ranged in age from nearly 200 years old to present-day samples.

Linear dimensions were measured using digital sliding calipers (Gedore No. 711 [150 mm] and Mitutoyo Digimatic [750 mm]). All bones of the left and right hind limb were measured three times, following which the average value was taken for each leg segment, with a further averaging of the left and right limbs. First, male and female birds were listed in different tables and pooled separately to examine whether there exists a dimorphism in specific bone and/or total leg length. This was not the case. The examinations were carried out at the Senckenberg Research Institute, Frankfurt am Main, the Bayrische Staatssammlung, Munich (both in Germany), the Museum of Natural History, Vienna (Austria) and the Royal Ontario Museum, Toronto (Canada).

Dissection of the pelvis and hind limb of lesser rhea, emu and ostrich

The complete pelvis and both legs of one adult male specimen of the lesser rhea preserved in formaldehyde were dissected macroscopically under laboratory conditions. In addition, identical body parts of two ostriches and three emus were dissected at ratite farms shortly after slaughter. For the slaughter birds, the mass of pelvic, thigh, and shank muscles, the collective leg muscle mass and the mass of the whole bird were routinely determined.

Results and discussion

The ostrich was chosen as a research model based on its exemplary abilities as a runner. We defined three base levels of functionality within this organism to find specialisations relating to its locomotional habits: 1) the scaffolding-level or skeleton, which provides the structural frame or "chassis" for 2), the drive mechanism level or musculature activated by 3), the energy synthesis and power distribution level or metabolism, which provides the muscles with energy to execute movement. In this paper we concentrate primarily on Level 1 and to a lesser extent, Level 2, and present specific examples concerning functional characteristics and their possible inter-relationships.

By means of comparative morphometric analyses, we examined the pelvic skeleton of *Struthio* and its large relatives, the greater and lesser rheas of South America, the Australian emu and the Southern cassowary of Northern Australia and New Guinea. With the exception of the solitary rainforest-dwelling cassowaries, the other relatively social ratites live in steppe-like and semi-arid regions with *Struthio* favouring savannah and desert environments. To place the large flightless ratites within a broader context, we also examined a smaller relative, the insectivorous kiwi, and included other non-passerine bird species whose different locomotional traits are well-researched and documented (Engels, 1938; Del Hoyo et al., 1992; Zeffer et al., 2003). This information provides valuable perspective on developmental specialisation among Aves, and serves as a useful comparative framework for assessing Struthioniform biology. With the exception of *Geococcyx*, these species are migrating birds and therefore excellent flyers. Since these birds primarily employ an aerial mode of locomotion with distinct endurance requirements, they possess specialised morphometric adaptations and divergently tuned metabolic relationships when compared to a flightless bird. Although this is an interesting offshoot, this study has focussed on 1) acquiring a diverse range of anatomical data to compare ratite to other non-passerine morphological patterns and 2) identifying and quantifying ostrich-specific adaptations unique within the ratite group.

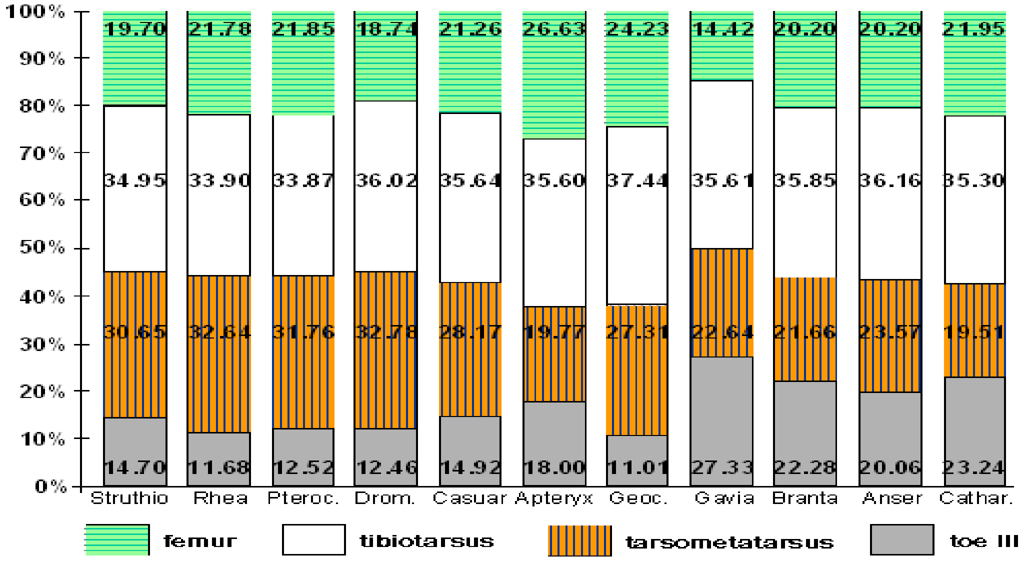
The smallest of the non-passerine birds investigated was the roadrunner, a cuckoo, which, with a mass of 230-340 g, has a greatly reduced size and scale compared to the Struthioniformes while leading a similar cursorial existence. The common loon (3600–5500 g) is an excellent diver and swimmer but is nearly incapable of bipedal terrestrial locomotion. The Canada goose (3000–4500 g) and snow goose (2300–2500 g) are good endurance flyers, swimmers and fairly good walkers. The turkey vulture (2000–2500 g), related to the stork, is a very good thermal glider that moves by walking or hopping sideways while on the ground.

Table 4.1.2.**1** Average lengths of all examined skeleton segments, total leg length (TLL) & ilium lengths (in cm)

Species	n	femur	tibiotarsus	tarsometatarsus	toe III	TLL	ilium
Struthio camelus	30	30.17	53.53	46.93	22.51	153.14	55.33
Rhea americana	21	21.05	32.76	31.55	11.29	96.65	28.38
Pterocnemia pennata	12	21.12	32.74	30.70	12.10	96.66	28.13
Dromaius novaehollandiae	10	21.78	41.87	38.11	14.49	116.25	36.16
Casuarius casuarius	6	22.14	37.12	29.34	15.54	104.14	36.73
Apteryx australis ssp	4	10.10	13.50	7.50	6.83	37.93	11.28
Geococcyx californicus	4	5.50	8.50	6.20	2.50	22.70	3.90
Gavia i. immer	4	5.54	13.68	8.70	10.50	38.42	14.08
Branta canadensis maxima	4	8.16	14.48	8.75	9.00	40.39	14.85
Anser c. caerulescens	4	6.90	12.35	8.05	6.85	34.15	11.60
Cathartes aura septentrionalis	4	7.37	11.85	6.55	7.80	33.57	7.43

Table 4.1.2.**1** shows the pooled measurement data of the functional length of each bone over a specific range of species. The data for total leg length equals the sum of all leg segments. It should be noted that this measurement does not exactly correspond to the actual hind limb length of a living bird due to the absence of cartilage and other soft tissues, but this difference is negligible. Since all samples were measured using equivalent criteria, the proportionality of results within the sample set should be considered valid. Based on the data collected above, the percentage of each bone length relative to total hind limb length was calculated (**Diagram** 4.1.2.**1**).

Diagram 4.1.2.**1**: Percentage of each bone segment in relation to total leg length
(values in % for each segment are given above its corresponding section).



According to the Law of the Pendulum, which states that a pendulum swings faster as its mass is concentrated closer to the pivot point (as in a metronome), we expected that the proximal parts of the hind limb of the ostrich would be relatively the shortest segments due to the proximal shift of limb musculature. On the other hand the lighter distal parts of the limb should be relatively longer with the exception of ground contact surfaces which, as usual in runners, are proportionally the smallest. This result was presumed not just in comparison to the other multi-locomotional species, but also within the relatively similar Struthioniformes. As shown in **Diagram** 4.1.2.**1**, the latter was not the case. The femur and especially the third toe of *Struthio* occupied a larger-than-expected proportion of the total leg length among the ratites.

To determine the significance of the ostrich's rather exaggerated third toe proportion, we decided to assess this skeletal structure as two distinct metatarsophalangeal elements, while maintaining consideration of its function as a 'foot' in the living animal. The proximal part (phalanx proximalis) was separated methodologically from the distal part (consisting of phalanges II to IV) which, in normal locomotion and stance postures, is always elevated above ground (including the minor phalanx I of the smaller fourth toe). This distal part is the de facto "foot" of *Struthio*, and represents the only actual ground contact surface while standing and during locomotion (along with the distal phalanges of the smaller fourth toe).

This peculiar supra-jointed toe posture has provided the ostrich with an additional biomechanical 'ankle', or, more accurately, a specialised elevated toe joint unique to *Struthio*. Considering the ostrich's pre-eminence as a runner, it is relevant to reference a similar unguligrade adaptation among horses. The further practical importance of this characteristic is illustrated by the fact that the strength of this joint is a relevant breeding criterion for farmed ostriches. A metatarsophalangeal joint posture deemed too close to the ground (or use of this joint as a ground contact point) is an indicator of weak hind limb constitution and the bird is considered to be unsuitable for further breeding (Kistner & Reiner, 2002). This feature of *Struthio camelus* represents a significant departure from common ratite and avian leg morphology. Practical biological applications of this structural aberration could include: effective shock absorption supporting 150 kg of body mass while running and an additional energy storage mechanism. This mechanism, identified in our study, supplements findings of elastic tendons in order to facilitate energy storage mechanisms, presented by Alexander (1984).

To return to **Diagram** 4.1.2.**1**, after adding the relative length of the phalanx proximalis (8.4 cm or 5.5 % of TLL) of the third toe of the ostrich to its tarsometatarsal length, to which it is functionally connected, all Struthioniformes adapted to a cursorial life and living in similar habitats now show quite equal values for their hind limb segment ratios. Furthermore, these apparently uniform total leg length values suggest that this group of ratite birds has achieved an optimal degree of cursorial specialisation in leg bone anatomy which cannot be further refined without influencing the whole organism in a drastic morphometric way in consideration of its mass and the gravitational forces acting upon it.

To support the general suppositions regarding hind limb dimensions and species specialisation in **Diagram** 4.1.2.**1**, we present some cursory interpretations of data gathered from the non-cursorial birds. Further work has been done e.g. by Zeffer et al. (2003).

The common loon has by far the relatively shortest femur and longest third toe, where the lengths of toe III as a representative for the length of the metatarsus is a good indicator of its function as a very efficacious webbed ‘paddle’ for swimming and diving against hydrodynamic resistance. On the other hand, the loon´s leg morphology appears predictably unusable for terrestrial locomotion. The two species of geese, being closely related, show quite similar values for their leg morphometry including a rather long third toe, which indicates a function of the metatarsus similar to the loon. But, being shorter than the loon´s metatarsus, it can also be effectively used for waddling terrestrial locomotion. All non-cursorial species possess a long tibiotarsus compared to the tarsometatarsus. The tibiotarsus, with its species-specific elongated Crista cnemialis, supports the musculature to drive an effective paddle in the common loon and geese and, in the case of the turkey vulture, provides the articulation required to grasp or perch. The specialisations of each species to its habitat are further reflected in other bodily subsystems, but are not the subject of this study.

As illustrated, all fast-running terrestrial birds exhibit increased tibiotarsal and tarsometatrsal length relative to total leg length in a proportion comparable to *Struthio*. There are no great deviations from this result among the examined specimens. All cursorial birds also possess a relatively decreased third toe length. This can be explained by the tendency of cursorial species to reduce distal elements, e.g. a reduction in the number of toes, in conjunction with 1) increased limitation to degrees of freedom to save muscle energy that would otherwise be used for controlling various segments and their joints and 2) reduction of masses in the distal segment. This is particularly true for *Struthio* which, as the only bird with just two toes, has taken this optimisation strategy a step further.

In combination with our quantitative separation of phalanx proximalis and distal phalanges of the third and fourth toe, we provide a solid morphometric validation for its position as the fastest biped. Its maximum functional “foot” length (toe III) amounts to 9.2% of total leg length (*vs.* 14.7% of TLL with undivided metatarsus: a 60% decrease), representing the smallest proportion in our sample. Initial parity of TLL % with *Casuarius* in **Diagram** 4.1.2.**1** is shown to be a misrepresentation due to insufficient consideration of actual functional applications. This difference can be reconciled by contextualising this second-largest ratite as an inhabitant of dense rainforests that tends to walk and hide rather than run while fleeing, as is common amongst its relatives. The cassowary’s relatively larger traction surface could also provide an advantage on muddy, unstable forest soil to avoid sinking and traction difficulties. A similar argument could be made for the kiwi’s proportionately large third toe value.

When assessing the ostrich´s relatively longer femur length, we must consider the typical avian posture with the knee highly flexed, placing the femur in a more or less horizontal position (muscle morphology – Level 2). With this postural disposition, the centre of mass is located in an area between the knee and the hip joint, or, in other words, somewhere along the horizontal axis of the femur, depending on the various degrees of movement in the stride cycle. In reference to this fact, we developed the hypothesis that femur length is influenced by the location of the centre of mass.

The femur in all birds is held in its position primarily by muscles inserting on the ilium, resulting in a compact ‘pelvis-femur-complex’. Because the femur is positioned horizontally and parallel to the pelvis, it is reasonable, from a functional perspective, to align this segment of the limb in relation to the ilium, rather than to the rest of the limb which is clearly orientated vertically and acts as the true pendulum.

By placing the femur in relation to the ilium, the relative result of femur lengths is *Struthio*: 0.55, *Dromaius*: 0.60. Thus, the ostrich femur is relatively the shortest in consideration of its functional relationship, as was expected. This limb arrangement achieves the desired result dictated by the Law of the Pendulum in concert with an organism's proclivity to conserve energy and optimise its biomass according to environmental imperatives.

It should be noted that linear measurements of leg bones of ratites have been collected before (e.g. Alexander, 1983; Gatesy & Biewener, 1991; Abourachid & Renous, 2000). When comparing data from these studies to the results shown here, some discrepancies were evident. For example, the relative length of the third toe of the kiwi and ostrich was identified as nearly identical in Abourachid & Renous (2000), each amounting to approximately 20 % of TLL (with the third toe of the ostrich undivided). As mentioned above, this proportion would be in contrast to the usual aim of cursorial animals to decrease traction surface and does not seem plausible. Furthermore, this high value for the third toe length shifts the relative dimensions of the remaining limb segments to an extent that other parameters in the kinematic chain, i.e. lever arms, momentum, and angles, would be drastically altered with unpredictable consequences.

When considering the functions of organism subsystems, it is important to maintain a clear perspective of the subject within its ecological context. As illustrated in the example of relative toe and femur length above, apparent peculiarities often reveal a practical application. In our dissection of the ostrich, we paid special attention to elements that limit or restrict degrees of freedom in the locomotor apparatus. A cursorial animal seeks to concentrate as much energy as possible on motion in the forward/vertical direction, which means that the locomotional pendulum should swing through a plane as efficiently as possible without excessive diversion of energy towards stabilisation of undesired sideways or horizontal movement. These limiting elements can be active, like muscles, which consume metabolic energy to exert force and suppress all movements of a joint which are not required for movement in a straight or preferred direction. Alternatively, these elements can be passive, like ligaments and cartilagenous structures with inherent densities and tensile properties that restrict or control movement. The latter elements are much more advantageous for a cursor than active elements as they require no expenditure of metabolic energy to achieve their function. We expected these structures to be prominently featured in ostrich morphology due to its noted qualities as an efficient runner within a fairly homogenous environment. Indeed, these passive elements were found in our dissection (e.g. Ligamentum iliopubofemorale, capsulare, and teres) and their existence is further validated by Firbas & Zweymüller (1971).

On the other hand, this tendency towards bi-dimensional stability leads to a relative limitation of manoeuvrability, as evidenced by comparisons between the ostrich and its close relative, the lesser rhea. These ratites are particularly capable of zig-zag manoeuvres and, like roadrunners, can run/flee with their necks extended forward through dense vegetation, change direction 180-degrees within a few strides and, in an instant, slip behind a bush to hide.

This is in contrast to their larger African relative, which always keeps its head erect, avoids high and dense vegetation and does not change direction in such a drastic manner. This does not mean that the ostrich is incapable of changing directions rapidly. By exploiting an extremity generally thought to be unnecessary in the locomotion of a flightless bird, the ostrich uses its relatively large wings as an "air-rudder" by quickly extending them while running.

This results in controlled turning and braking manoeuvres and compensates for a lack of lateral articulation in its legs. However, the more stable *Struthio* will rely primarily on its speed and endurance to avoid potential harm or to travel great distances over flatlands to seek new sources of food, water, or territory.

When interpreting the active elements or muscle functions it is essential to consider the associated tendons, functional pathways and fusions with other tendons and/or muscles. Few morphological investigations of the ostrich musculature contain functional interpretations. (Gangl, 2001; Weissengruber et al., 2003). As is well known, the M. ambiens is connected to a toe flexor and thereby forms a kinematic connection from the pelvis to the third toe. It is very likely that this fusion could also help to save energy and stabilise the whole limb since this muscle pathway leads from the medial anterior pelvis to the lateral tibiotarsus, where the originating M. flexor perforatus digiti III runs down to the metatarsus and inserts at the third toe posteriorly.

But ostriches are not the only birds possessing this particular muscle pathway, nor is the fusion to toe flexors unique to *Struthio*. A great diversity of bird species of all sizes and habitats exhibit this feature, so the functionality of the M. ambiens apparently differs according to the particular environmental context of each species. Surprisingly, emus do not have a M. ambiens at all, but lead a lifestyle quite similar to the cursorial ostriches. In other instances, the absence of muscles is a form of optimisation that may not be immediately appreciated. This is the case in the ostrich, where two reductive advantages for a cursorial life co-exist: with the reduction of the 1st and 2nd toe the traction surface was minimised and the muscle and connective tissue required for these toes was also reduced (except the M. flexor hallucis longus). These muscles, if present in other birds, originate at the distal, swinging parts (tibiotarsus and tarsometatarsus) of the limb, slowing it down according to the Law of the Pendulum. These contrasting examples illustrate the challenge involved in determining the true function of complex muscle groupings and inter-muscle fusions, especially when more than a single joint is influenced. To complicate matters further, it is difficult to isolate a single muscle and describe its absolute function with total clarity. All musculature within a living system exists in a finely tuned web of interdependency, with movement in an apparently distant quadrant of the organism reflected in compensating reactions in another area: this fluidity becomes more pronounced among closely grouped muscle masses. This biological complexity exists in stark contrast to purely mechanical systems, where predictable material rigidity, finite degrees of movement and absolute energy input/output equations quantify these ergonomic issues with great eloquence and finality. As a starting point towards resolving some of these challenges, we are able to reliably gather data on raw muscle masses. Although this can show us a great deal about the potential energy of the muscle, we must never lose sight of the muscle's context within the organism when interpreting function.

As mentioned above, the muscle masses in the limb of a cursorial animal are typically situated proximally to the body and as close to the pivot point (or leg or hip joint) as possible to optimise pendular facilities and manage inertial forces. The muscle mass distribution of the limbs in *Struthio* and *Dromaius* was investigated from this viewpoint. First we calculated the masses of all limb muscles based on the Australian cut and the Kulmbach cut. These standardised cuts for slaughtered ostriches explain how specific muscles should be cut from the carcass and define their mass and quality (e.g. tenderloin, steak). Our measurements were done at the Gayer Ostrich Farm, Hohenaltheim/Bavaria on two carcasses using the Kulmbach cut.

The results were identical with the standard (**Table** 4.1.2.**2**).

A cutting scheme for emus was not available, therefore three emus at the Schneider Emu and Rhea Farm Ansbach/Bavaria were examined using the Kulmbach cut. The results of all leg muscle measurements showed no significant aberrations among the sample set so our standardisation can be considered valid. All data is shown in **Table** 4.1.2.**2**.

Figure 4.1.2.**1**: Carcass of ostrich
(A = Pelvic + thigh muscles
B = shank muscles)

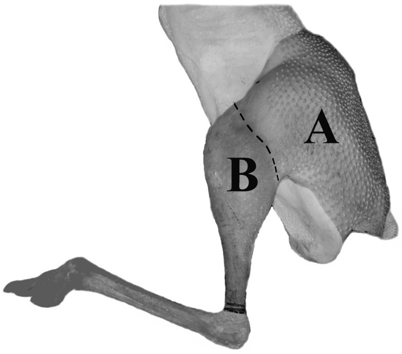


Table 4.1.2.**2**: Mass of muscle portions (tbw = total body mass; all data in kg)

Species (source)	tbw	A+B	A	B	A : B
Struthio camelus (Australian cut)	100	30.52	19.12	11.40	1 : 0.60
Struthio camelus (Kulmbach cut)	80	23.77	14.65	9.12	1 : 0.63
Struthio camelus (own data, n = 2)	100	30.29	18.55	11.74	1 : 0.63
Dromaius novaehollandiae (own data, n = 4)	40	11.19	6.53	4.66	1 : 0.71

This morphological examination produced evidence that the mass distribution at the muscular parts of the limb differs between emu and ostrich. The relationship of pelvic and thigh muscles (**A** in **Fig.** 4.1.2.**1**) to shank muscles (**B** in **Fig.** 4.1.2.**1**) amounts to a difference of about 10 % at a nearly equal proportion of total limb musculature (sum of **A** and **B**) to total body mass in both species (approx. 28 % in *Dromaius* and approx. 30 % in *Struthio*). This signifies that 1) in comparison to the emu, the ostrich shifted 10 % of its muscle mass proximally and towards the pivot point of the pendulum and concurrently, 2) the shank or swinging part has to carry 10 % less mass than the tibiotarsus of the emu.

In the ostrich, this strategy of mass distribution reflects an optimisation towards fast endurance locomotion. On the other hand, a powerful shank musculature, i.e. the M. gastrocnemius improves the capacity for rapid acceleration as well as manoeuvrability. Indeed, the M. gastrocnemius of the emu has been found to be highly efficient concerning structural and metabolic characteristics by Patak & Baldwin (1993) underlining our findings of raw mass distribution towards an optimisation for sprinting and manoeuvrability (emu) versus endurance (ostrich).

Conclusions

The structural design of the hind limb among the large ratites appears to have reached a maximum state of optimisation towards achieving fast terrestrial locomotion. Due to the predominantly uniform nature of large Struthioniform leg anatomy, subtle differences and specialisations within this baseline group can be reliably isolated and compared to reveal specific functions, applications and their tangible effects. Verifiable conclusions may be less obvious among other more diverse sample groups. In validation of our methodological approach, this study illustrates that form and function must be regarded as coexisting and co-dependant, and that form has limited meaning when divorced from its functional expression. In the worst cases, assessment of de-contextualised or disembodied materials can lead to faulty interpretations of function. For instance, we have shown that relatively short femurs are desirable for rapid locomotion, but it does not necessarily follow that all species with short femurs are excellent runners, as evidenced by the common loon's inability to walk. This result has particularly important consequences relating to the interpretation of the fossil record.

Due to this uniform pattern in limb anatomy of the large Struthioniformes, species-specific anatomical discrepancies are evident in comparisons between the emu and ostrich, inferring differences in locomotional behaviour. In particular, the emu possesses characteristics favouring higher manoeuvrability and acceleration capacities when compared to the ostrich. Its traction surface is larger and its three relatively longer toes enable the emu to get a better grip on the substrate to avoid slipping. These advantages towards acceleration ability are supported by a shift of muscle masses towards the M. gastrocnemius.

On the other hand, the ostrich shifted its limb masses proximally towards the trunk to optimise its swinging features – important for endurance locomotion. It also shortened its traction surface drastically by integrating parts of the metatarsus into the tarsometatarsus and therefore elongating the latter. This supra-jointed toe posture probably increases energy storage in correlation with elastic tendons.

Generally, active limb control elements in *Struthio* were presumably replaced for the benefits derived from passive elements to a greater degree than in other large ratites. The result would be a lower cost of energy for stabilising the limb during locomotion, allowing increased efficiencies in the forward/vertical direction.

Relatively large traction surfaces, necessary for manoeuvrability and acceleration are diminished in favour of optimisation for endurance locomotion, with the further consequence of a total reduction of the second toe in the ostrich. However, a reduction of the fourth toe, as seen in unguligrade mammals such as the horse, is not to be expected for the ostrich which needs this toe to maintain a stable bipedal stance.

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4.1.3 Statics

The maintenance of static equilibrium is an essential component in the success of any organism. Without balance, locomotion is impossible. In order to maintain static balance, an organism must ensure that the vertical projection of the Centre of Mass (CoM) remains within its Base of Support (BoS) which consists of the plantar surface of all ground contact elements (e.g. feet, toes, hooves) including the resulting polygonal area defined by those elements (e.g. Hof, 2008; Vogel, 2003). Thus, a quadruped stands very stable on four legs (like a table) with its CoM well within the resulting large BoS. Maintaining static balance in a biped with an obviously much smaller BoS presumably requires more specialised strategies to manage CoM. For standing humans, these strategies involve muscular and nervous control mechanisms (e.g. Hof, 2008) and standing posture *per se* (Kummer, 1956). Similar mechanisms are certainly also found in standing birds. However, in addition to these active components, the physical *bauplan* of an organism will likely complement balance passively.

In his anatomical-physiological study about avian hind limbs, Stolpe (1932) argues that the pelvic anatomy of the ostrich represents the statically most optimised construction when compared to any other avian species and that the ostrich acetabulum (i.e. hip joint) is positioned most centrally in the trunk. In combination with a short, horizontally held femur, the resulting lever arm through which the upper body mass of this heavy bird acts on the hip joint is rather small. This avian-specific arrangement likely decreases muscle power required to stabilise hip and knee joint against over-flexion during stance where consequential bending moments acting on the avian femur are structurally compensated by its short length and robusticity (e.g. Biewener, 1982; Gatesy, 1991; Maloiy et al., 1979; Stolpe, 1932). The need to counteract over-flexion results from the fact that, in terrestrial bird species, the CoM is located rather cranially relative to the acetabulum with the consequence that the ground reaction force (GRF) exerts a flexing moment towards the hip joint during static standing (Manion, 1984). Especially in ratites, the CoM – through which the GRF acts on the body during standing – appears to be positioned particularly cranially (Abourachid & Renous, 2000; Alexander, 1983; Fedak et al., 1982; Rubenson et al., 2004). Economic standing positions through enhanced static stability may constitute an important factor in the net energy budget of the ostrich especially when considering that Bertram (1992) showed that feral specimens spend several hours per day standing and walking relatively slowly. In order to examine whether the proposed beneficial hip position (Stolpe, 1932) does indeed exist exclusively in the ostrich, we compare morphometric data of trunk, ilium and femur of nine non-passerine bird species, including four cursorial species in the first part of this unit.

Hip position alone is not sufficient to speculate whether a biped stands relatively balanced. In the second part, the entire limb is functionally rejoined with the trunk and orientation of trunk/ilium and limb segments/crural joints will be incorporated within a more inclusive scheme based on observations of live specimens and video footage. This allows estimation of the extent to which dimensions and orientation of skeletal elements affect static stability in cursorial bird species of differing size and mass.

Materials and methods

Linear lengths of trunk, ilium and femur of nine non-passerine bird species, with n = 103 (Chapter 4.1.2, i.e. Schaller et al., 2005), have been collected. Position of the acetabulum within the ilium was determined for each species. Subsequently, the ilium was schematically reduced to its linear length and positioned within total trunk length. Trunk lengths were obtained from literature and moulds examined at the ornithological collections of the Royal Ontario Museum (Toronto, Canada) and the Research Institute Senckenberg (Frankfurt/M., Germany). All data were combined and normalised to identical scale (**Fig.** 4.1.3.**1**). Secondly, spinal column and pelvic limb segments were included and oriented as seen in the live standing ostrich, lesser rhea (*Pterocnemia pennata*), kiwi (*Apteryx* sp.) and roadrunner (*Geococcyx californicus*) respectively.

Linear lengths of the pelvic skeleton were obtained from Chapter 4.1.2. Data of standing positions was rendered from observations of live specimens for ostrich, rhea and kiwi and own video footage of rhea and ostrich. Additional documentation of *in vivo* postures was used from literature for the kiwi and compared with Abourachid & Renous (2000).

Results and discussion

Fig. 4.1.3.**1** depicts a simplified model with femur and ilium/trunk as a straight linear axis. As seen in limb segment dimensions (Chapter 4.1.2), all large ratites are very similar in possessing a relatively long ilium with the ostrich exhibiting the relatively longest ilium (**Fig.** 4.1.3.**1**). The kiwi, as the smallest and lightest ratite, has a different acetabular position than its larger relatives with its hip joint located most caudally. This situation is comparable to the roadrunner, the smallest of the investigated cursorial birds, which exhibited an even shorter ilium.

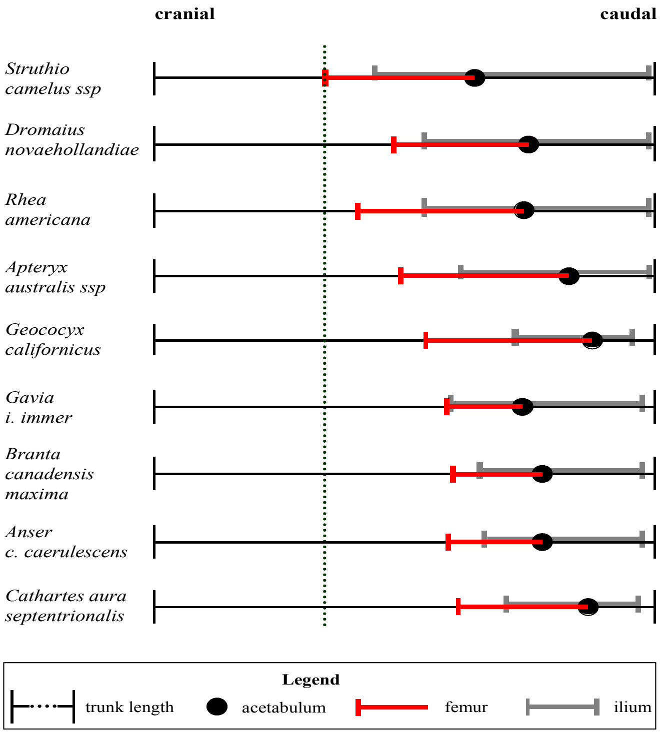

Fig. 4.1.3.**1**: Linear relationship of trunk, ilium and femur length and relative position of acetabulum.

The similar physical appearance of water birds (snow goose, Canada goose and common loon) was reflected in similar ilium and acetabular position – while their similarity in limb segment lengths has been shown in Chapter 4.1.3 with functional interpretations provided by e.g. Abourachid & Renous (2000) and Zeffer et al. (2003).

Concerning Stolpe’s (1932) proposition about relative acetabulum position in the ostrich, it could be seen that, although the acetabulum is most cranially positioned in comparison to the other species of the sample group, it is not situated at the horizontal mid-point of the trunk in lateral view. The knee, however, does appear to be located centrally. Since the knee is the *de facto* origin of the vertically oriented swinging part of the limb, this orientation may be more advantageous for balancing the trunk than placement of the acetabulum in the centre of the trunk. Stolpe's (1932) proposition would result in a cranial shift of the knee, increase the flexing moment acting on the hip, probably altering requirements for muscular support of trunk mass with unknown consequences to overall posture.

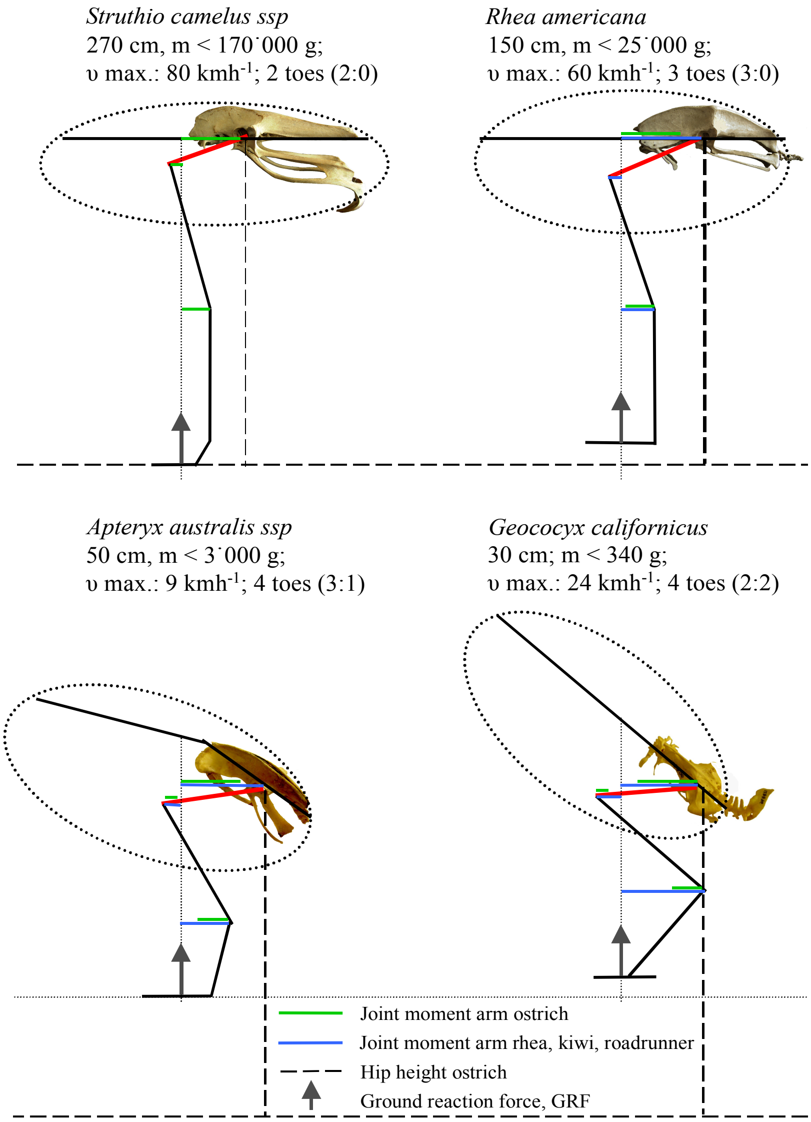

Fig. 4.1.3.**2**: Illustration of orientation of body axis and limb segments.

However, **Fig.** 4.1.3.**1** provides only a linear-horizontal scale and examination of this suggestion requires the more naturalistic model shown in **Fig.** 4.1.3.**2** where relative forces acting on the limb joints can be estimated. These schemes incorporate actual pelvic skeleton, limb segment dimensions, *in vivo* standing postures and include additional factors relating to body mass, toe number and running speed. The smaller kiwi and particularly the smaller roadrunner feature a vertebral column that is oriented rather vertically. By comparison, the vertebral column of the ostrich is oriented perfectly horizontally and somewhat less horizontally in the lesser rhea. The orthogonal orientation of trunk relative to limbs reflects a statically optimum precondition in which a relatively heavy beam, i.e. the trunk, can be more easily balanced when oriented horizontally on top of two vertically oriented struts (e.g. Kummer, 1956). This is particularly important when the beam/trunk is located far above the ground (1 to 1.5 m in the ostrich). The lighter kiwi and much lighter roadrunner, with CoM located much closer to the ground, apparently do not rely on similarly economic statics because much smaller GRFs act on the joints which, in turn, result in smaller torsional moments. This is most evident in the roadrunner which exhibits a very different pelvic architecture from the large ratites. First, the sacral vertebrae are longer to provide an insertion area for the long tail feathers which serve as a stabilizer and rear rudder for this small running bird. Secondly, the caudal pelvic wing of the cuckoo faces downwards as opposed to the vertical orientation seen in ratites while the postacetabular ilium provides the main area of origin for hip extensor muscles which are presumably most active during push-off (e.g. Gatesy, 1999). This difference may be partially explained by its particular genealogy and/or by the obvious difference in overall limb posture and mass. The relatively short ilium certainly reflects a reduced need for powerful musculature to support the trunk in this relatively light bird. As shown in various allometric studies, muscle force is directly related to muscle diameter. As muscle diameter increases in cross section (area), the total volume of the muscle increases cubically with the relationship between power output and mass becoming generally disadvantageous in larger organisms (e.g. Schmidt-Nielsen, 1984). Compared to the cuckoo, the rhea – and particularly the ostrich – must carry comparatively larger trunk loads requiring proportionately greater muscle mass that, by extension, requires a larger surface area for pelvic muscle attachment. The predominantly vertically oriented iliac and ischiac wings of the ratite pelvis can be interpreted in the context of the small interacetabular distance (Firbas & Zweymüller, 1971) which provides close positioning of the limbs – a common characteristic in cursorial species (**Fig.** 4.1.3.**3**).

When focusing on the pelvic bone as a whole, the ostrich possesses the longest ilium. In the framework of this study, the evolutionary progress can only be speculated. It could be the result of an elongation of the postacetabular pelvic portion (**Fig.** 4.1.3.**1** & **2**) or a cranial shift of the acetabulum or a combination of the two 'mechanisms'. For the extant ostrich, this elongation might alter areas of origin of pelvic muscles (Chapter 4.1.2) when compared to the more compact pelvic bone of the closely related rhea which is smaller and less advanced as an endurance-runner. The caudal attachment may influence tractive/pulling directions of the originating musculature – predominantly the extensors of hip and to a certain degree of the knee (Chapter 4.1.1). These muscles are presumably most active during push-off which must be very powerful in this cursorial biped to achieve suitable thrust during running. It may also be that this pelvic architecture provides a larger muscle attachment area as might be concluded from the proximal concentration of crural muscle mass. As a first experimental step, this would require measurement of actual pelvic bone surface (e.g. with 3D scanning technology).

However, it is difficult to hypothesise whether the caudally elongated ilium was the evolutionary cause or the consequence of locomotor performance and/or a proximal shift of musculature in the largest and heaviest extant bird. In addition to the need for increased or altered muscle attachment area, the long postacetabular ilium may also reflect a specialisation of the air sack system.

Another reason – or cause – for the long ilium/pelvis may be offered by the relatively long, horizontally oriented trunk. Besides providing powerful push-off, postacetabular muscles support the weighty trunk relative to the distal limb. Concerning muscle power output, Smith et al. (2006) conclude that in comparison to the horse, ostriches possess more short-fibered pelvic muscles as a consequence of having to support trunk mass. Viewed from a functional perspective, this poses an unsurprising result considering that the bipedal ostrich must achieve with two limbs what the horse can accomplish with four.

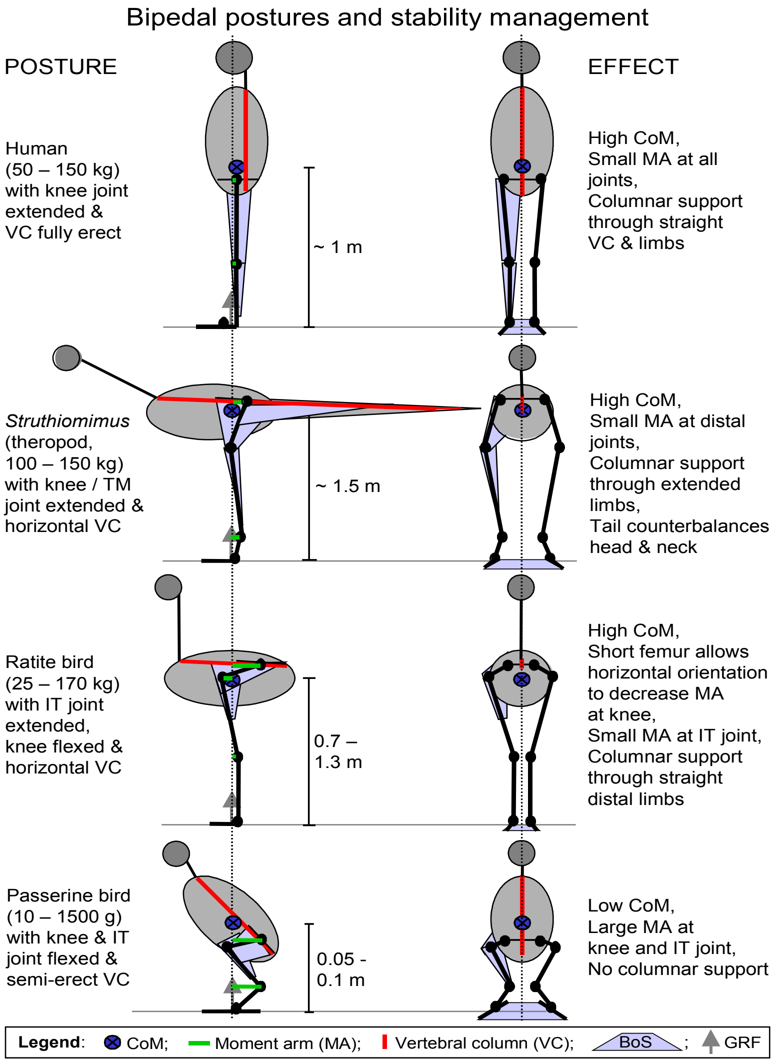

Fig. 4.1.3.**3:** Schematic of bipedal standing postures depicting basic interrelationships of CoM, BoS, vertebral column and limb orientation; TM refers to tarsal joint, IT to intertarsal joint.

The ostrich limb has the longest effective limb length within the sample group (**Fig.** 4.1.3.**2**). Long limbs have been generally acknowledged as a beneficial attribute to achieve greater step lengths (Preuschoft & Christian, 1999). However, the relative limb length also depends on the extension radius of a species' limb. This factor cannot be evaluated with skeletal material alone and is carried out as part of the functional analysis with intact anatomical and live specimens (Chapter 4.2.1). The effective limb length difference between rhea and ostrich is achieved largely through the elevated metatarsophalangeal joint of the ostrich.

When assessing limb posture, a major difference between the differently sized birds, especially ostrich *versus* roadrunner, is the orientation of the intertarsal joint. While oriented nearly straight in the large, long-legged ostrich and rhea, it is fairly flexed in the much lighter kiwi and roadrunner. As shown for the four species presented in **Fig.** 4.1.3.**3**, the lever arms acting on the limb joints increase with decreasing body mass/dimensions. This can be explained by the fact that with the CoM located closer to the ground, the muscular power required to act against joint moments/lever arms decreases as well. In reverse, a larger animal must ensure that moment arms, as well as torques (not shown here), are kept small to increase self-stabilization of the limb for efficient stance postures. In this context, passive constraints and kinematics of the intertarsal joint will be analysed in Chapter 4.2.2. As in humans, which stand with an extended knee to provide columnar support for their body mass, larger and heavier birds stand with an extended intertarsal joint. A valid future project would entail a comparative study correlating lifestyle, body mass, limb segment dimensions and intertarsal joint posture in avian species to classify the interplay of these factors.

While overall dimensions are largest in the ostrich, it appears to have the smallest ground contact surface with only two partly elevated toes. In combination with a small interacetabular distance (i.e. narrowly placed limbs), these structural preconditions result in a relatively small BoS which would appear to be disadvantageous to the maintenance of static stability (**Fig.** 4.1.3.**3**). To the contrary, this small BoS is a morphological cornerstone in the mechanics of ostrich locomotion. The specific interaction of toes with substrate will be functionally analysed in detail in Chapter 4.2.3.

Concluding remarks of Chapter 4.1

With data extracted exclusively from anatomical specimens it is possible to identify structural attributes involved in the efficient, fast locomotion of the ostrich. The orientation of the trunk and its relative position to the hind limbs reflects a condition of optimised statics in the heavy ostrich, complemented by an overall limb orientation which, due to short moment arms, reduces moments acting on the joints, particularly at the distal intertarsal and metatarsophalangeal joint. This in turn reduces the need to stabilise the distal joints using muscle power and allows for a proximal shift of musculature towards the pivot point of the hip joint to optimise the swing capacities of the limb in combination with light, elongated distal limb elements (as shown in Chapter 4.1.2). Musculature itself is often bi-articular and/or functionally interconnected to channel power-output in a directed manner towards motion in the fore-aft plane during swing phases. This condition is presumably supported by a stringent guiding/constraining passive locomotor system. In combination with the interconnected muscle-complexes, this condition may guide overall limb segment motion and ensure proper placement of the phalanges on the substrate to affirm stable grip and concentrate muscular force for powerful propulsion at toe-off. However, these predictions can only be examined by comparing morphological data with *in vivo* actualities (see Chapter 4.2.1 to 4.2.3).

The correct mounting of display skeletons is crucial. Incorrect limb postures have been observed where the intertarsal joint is flexed to a much greater degree than is the case in a live standing ostrich. In some collections, the metatarsophalangeal joint touches the ground plane – maybe because the preparator/taxidermist observed zoo specimens and was misled by the typically weak metatarsophalangeal joints (own observations) of captive ostriches. In at least one case, the entire distal limb is anatomically incorrect with the 4th toes placed medially – as opposed to laterally – in respect to the 3rd toe. Analysis and reliance on improperly presented anatomical specimens probably leads to false interpretations about locomotor behaviour. Applying anatomical-physiological methods with observation of live specimens prevents these misconceptions and renders a more suitable backdrop for accurate interpretation of locomotor function.

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4.2 Biomechanics and locomotor dynamics

The muscular complex actively converts metabolic energy to initiate controlled limb movement for locomotion. However, limbs also contain a passive management system comprised of a cohesive combination of ligaments, cartilage and other connective tissues. The interplay of these elements with skeletal anatomy, especially through the locus of the joints, manages motion passively without the metabolic expenditure associated with muscle power. A basic hypothesis in this study is that, in a fast long endurance runner such as the ostrich, the passive system constrains the action radius of locomotor elements to a very high degree especially when compared to the comparatively free range of limb motion found in humans.

This passive control system allows muscle power to be focussed mainly towards forward propulsion by swinging the leg in the fore-aft plane without the metabolic cost associated with multiple positional corrections, avoidance of over-extension and management of excessive limb segment displacement in the lateral plane. The ligamentous apparatus in combination with joint processi also contribute limb stabilising qualities that are an important energy management factor in the long-legged, heavy ostrich. Here again, conserving muscle power by passively supporting the joints, and thus body mass, is highly beneficial for the energy budget of an animal that spends 96% of waking time standing, walking or running (Bertram, 1992). In this context, the function of the most distal part of the limb, the toes, is of great interest. As the sole elements of ground contact, researching the load bearing capacities of the phalanges and their anatomical adaptations towards the substrate should increase the understanding of ostrich locomotion.

In the first chapter of this unit, the overall constraining qualities of the passive locomotor system and its effect on joint mobility will be quantified and anatomically qualified. Stringent limitations to limb manoeuvrability become obvious when observing the ostrich. Unlike the closely related emu, it cannot kick in the rearward direction, nor can it voluntarily flex its phalanges to grasp in the manner of any perching bird. An ostrich cannot scratch its head like most other avian species and must instead bend its neck to bring the head down to the level of the toes. Taken together, the many constraints to ostrich limb motion range seem to suggest a sacrifice of certain common articulations to achieve efficient locomotion over long distances.

In the second chapter, the ligamentous system of the intertarsal joint will be described and functionally analysed in detail and re-contextualised with live kinematics. In the third chapter, a first-time examination of ostriches performing at various speeds depicts *in vivo* toe function in relation to the substrate.

4.2.1 Constraining/guiding qualities of the passive locomotor apparatus

The passive structures responsible for abduction control in the hip joint have been examined in detail by Firbas & Zweymüller (1971). Considering the trunk mass (incl. neck, head and wings) of 60 kg –100 kg in adult ostriches, luxation of the femora must be prevented to ensure that the ostrich can support its body mass. As demonstrated by Firbas & Zweymüller (1971), this structural integrity is achieved by the presence of three strong ligaments. Once all pelvic and femoral muscles were removed, the abduction of the femur was restricted to the same degree as with muscles attached, providing that the Ligamentum capsulare and Ligamentum iliopubfemorale remained intact. Abduction of 60° was possible after cutting the Lig. capsulare but the Lig. teres prevented any further lateral motion. Once the Lig. teres had been cut, a further limitation to lateral motion was delivered by the trochanter-antitrochanter articulation whose importance as a structural attribute in bipedal locomotion is also addressed by Hertel & Campbell (2007).

The knee joint is also managed by a complex ligamentous system. As in all bird species, the knee of the ostrich is formed by femur, tibiotarsus and fibula. A very thorough examination of the interplay of knee ligaments by Fuss & Gasser (1992) described the functional expression of the knee in the ostrich by stating: "…the cruciates serve the guiding of the joint and the restriction of motion, whereby the majority of the cranial cruciate fibres are taut in extension while those of the caudal cruciate are in flexion." This finding is supported in the present inquiry where data from the isolated hind limb is integrated with data from live subjects and shows the consistency of maximum extension angles among all sample groups. This result reflects the restrictive capacities of the cranial cruciate fibres in the ostrich knee.

The ligamentous system of the metatarsophalangeal joint and phalanges in the ostrich have been documented in great detail by Gangl (2001). In addition to a description of the extensive fibrous encasement of the phalangeal joints, Gangl addresses a ligament-driven tendon-locking mechanism that stabilises toe flexion without active power expenditure during stance.

The passively guided 3D-axis alignment in the intact limb joints of ostriches has been documented by Rubenson et al. (2007). Using unloaded isolated limbs of anatomical specimens he shows that "...both the knee and ankle (intertarsal joint, author's note) exhibit coupled internal/external and abduction/adduction (varus/valgus at knee) rotation with passive flexion/extension". Furthermore, Weissengruber et al. (2003) reported that in isolated ostrich legs all distal joints are actuated within the obligatorily combined chain of limb segment motion. Within this interconnected multi-jointed muscle-tendon system, manual extension/flexion of the knee also leads to automated 4th toe ab-/adduction relative to the major 3rd toe (Schaller et al., 2007). This lateral 4th toe positioning is mainly managed by an interphalangeal ligament, which leads to ab- or adduction dependant on 3rd toe extension/flexion (Chapter 4.2.3).

Specific data pertaining to the ligaments of the intertarsal joint appear in the historical scientific record but lack the required detail, data and functional interpretation for inclusion in the present study. A thorough anatomical/kinematic survey of the intertarsal joint is presented in the next chapter.

This chapter presents quantification of passive limb constraints in the fore-aft plane by comparing the articular motion range of anatomical specimens with that of live ostriches.

Materials and methods

Joint motion range in dead ostriches

Five ostrich cadavers from local breeders were used in the course of this experiment (**Table** 4.2.1.**1**). Motion range measurements for the intact ostriches were carried out on-site where maximum flexion/extension angles for all limb joints were recorded. The ostriches, slaughtered less than five minutes prior to measurement, were positioned in a specifically designed suspension device attached to a mechanical hoist with the ilium positioned horizontally to mimic the over-all trunk orientation of a live standing bird. The limbs were fully mobile to allow manipulation in the fore-aft plane to gather maximum flexion and extension angles of all limb segments. To gain qualitative insight into over-all lateral displacement and possible influences on the following kinematic examination, each limb element was also manipulated to its maximum lateral excursion limit.

Table 4.2.1.**1: Ostrich specimens in manipulation experiments**

ostrich	1	2	3	4	5
gender	m	m	M	m	f
age	14 months	14 months	5 years	15 months	14 months
body mass	105 kg	115 kg	150 kg	105 kg	90 kg

Subsequently, the legs of two ostriches were obtained for reductive dissections performed at the Senckenberg Research Institute, Frankfurt/M. (Germany). Under lab conditions, muscles were removed from the hind limbs and the pelvic-limb complex was manipulated to determine the ability of ligaments and cartilage (passive structures) to limit fore-aft motion. At both sites, two digital video cameras recorded the front and lateral view of the manipulations and VirtualDub software was used for detailed analysis of minimum/maximum flexion/extension. In addition, a protractor/goniometer was used in the lab to measure degrees of freedom *in situ*.

Data acquisition of joint motion range in live ostriches

To determine the maximum extension and flexion angles of the intertarsal joint in live ostriches, we gathered kinematic data for walking to intermediate running speeds ranging from 0.5 ms^{-1} to 4 ms^{-1}. Since the focus was maximum joint excursion angles during all modes of locomotion, the data from walking and running has been pooled. The methodology of angle measurement/limb axis alignment was identical to the orientations employed in the motion range measurement of dead ostriches (Chapter 4.2.2, **Fig.** 4.2.2.**2**).

Experiments were carried out with two 3-year-old females (90 kg) and two 13-year-old males (130 & 150 kg) in a levelled-ground corridor (76 m long & 3 m wide) which was separated from their main outdoor-enclosure by coarse wire mesh. Knee, intertarsal and metatarsophalangeal joints were marked by applying locator marks (4 cm in diameter) with aluminium spray. This spray, generally used in animal healthcare as a disinfectant, is clearly visible on film and cannot be removed by the ostriches. Two digital video cameras (Canon MV 500i & 900, 50 frames/s) were oriented at a 90° angle to capture front/back and lateral view simultaneously with the cameras installed at a distance of 5 m from the subject, synchronised using time-code. The experiment set-up is equivalent to the one used in Chapter 4.2.3. At least two complete stride cycles were recorded at each pass.

In addition, one camera (Canon MV 500i) captured lateral close-up view of the distal limb (knee joint to toes) with special emphasis on the dynamics of the intertarsal joint. Only walks and runs that remained straight for at least three stride cycles were included in the data pool, as verified by the frontal/dorsal view camera. Out of 69 recordings which were yielded in total, five straight walks (duty factor: ~ 0.65; ~ 1 ms^{-1}) and five straight runs (duty factor: ~ 0.5; 3 – 4 ms^{-1}) were selected for analysis. VirtualDub and Didge Digitizing software (Allistair Cullum) were used to compile and analyse the video sequences.

Results

The following **Table** 4.2.1.**2** contains the pooled data for the articular motion range measurements (top section). The overall excursion for all set-ups is depicted in the central section, followed by the final comparison between maximum flexion/extension angles of anatomical specimens and live ostriches.

In live ostriches, the difference between maximum flexion and extension angle at the joints increased progressively on a proximodistal gradient (**1a Difference flex./ext.**). As expected for a cursorial animal, the femur is far less involved in maximising the swing plane than the distal elements, which is reflected by the comparatively small excursion angle at the hip joint. This can be explained when considering the morphology and morphometry of the entire leg. As shown in Chapter 4.1.2 (morphometric analysis), the power generating muscle mass is concentrated proximally at the pelvis and horizontally oriented femur while the vertically oriented distal limb elements are rather long and light and mostly operated by tendons (Chapter 4.1.1, morphology). The distal increase of excursion angles was most pronounced in running trials with maximum values for joint movement occurring at 4 ms^{-1}, reflecting the highest speeds measured (see also following Chapter 4.2.2 for graphic illustration of walking *vs.* running kinematics).

Table 4.2.1.**2: Fore-aft range of joint motion**

	hip joint		knee joint		intertarsal joint		metatars. joint	
	flex.	ext.	flex.	ext.	flex.	ext.	flex.	ext.
1a Locomotion/1 – 6 ms^{-1} (n=10)	*35.0°**	*60.0°**	80.0°	135.0°	65.0°	168.0°	60.0°	264.0°
1b Sitting	20.0°	/	48.0°	/	20.0°	/	145.0°	
2 Dead (skin + muscles)	20.0°	75.0°	46.6°	135.4°	19.6°	168.0°	56.0°	264.0°
3 Dead (ligaments only)	20.0°	80.0°	34.0°	136.0°	10.0°	168.0°	54.0°	270.0°
1a Difference: flex. to ext.	*25.0°**		55.0°		103.0°		204.0°	
2 Difference: flex. to ext.	55.0°		88.8°		148.4°		208.0°	
3 Difference: flex. to ext.	60.0°		102.0°		158.0°		216.0°	
1b – 2 Difference	0°	/	1.6°	/	0.4°	/	89.0°	119.0°
2 – 3 Difference	0°	5.0°	12.6°	0.6°	9.6°	0°	2.0°	6.0°
1a – 2 Difference	15.0°	15.0°	33.4°	0.4°	45.4°	0°	4.0°	0°
1a – 3 Difference	15.0°	20.0°	46.0°	1.0°	55.0°	0°	6.0°	6.0°

* obtained from Rubenson et al. (2007)

The slight difference in flexion values for samples with muscles intact vs. limbs with muscles removed (**2 – 3 Difference**) results from the presence of musculature that acts as a physical obstacle to prevent further flexion. When comparing live kinematics with articular mobility of anatomical specimens (**1a – 2 & 1a – 3 Difference**), considerable discrepancies in motion range occurred for knee and intertarsal flexion while maximum extension remained fairly consistent. The proximal hip joint showed similar excursion values among *in vivo* measurements and anatomical specimens. The most-distal metatarsophalangeal joint exhibited the lowest angular deviation.

Maximum flexion values for hip, knee and intertarsal joint were similar in intact anatomical specimens and live sitting ostriches (**1b – 2 Difference**). Only the metatarsophalangeal joint remained in a mid-range position since this posture places the soles of the toes flat to the ground to serve as a support area in tandem with the caudal side of the intertarsal joint. For this purpose, the latter is dorsally strengthened by massive layers of cartilaginous sheath, connective tissue and thickened skin.

In the course of the manipulation experiments, it could be observed that flexion/extension was coupled to internal/external rotation in femur, tibiotarsus and tarsometatarsus. Abduction/adduction of the femur was possible with the hip in flexed position and decreased as the hip joint was extended. Similarly, it was possible to rotate and ab-/adduct tibiotarsus with fibula when the knee was in an intermediate state of flexion of 100° ± 5°. Conversely, when the joints were fully extended, mediolateral dislocation or internal/external rotation was highly restricted and practically impossible in the intertarsal joint.

Fig. 4.2.1.**1a** depicts the fore-aft maximum motion range of all limb joints as measured in anatomical specimens where only ligaments were left intact. **Fig**. 4.2.1.**1b** shows the overall position of the limb in three main stages of a stride cycle in an ostrich running at 50 kmh^{-1}.

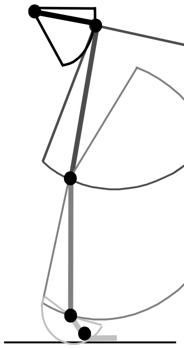

Fig. 4.2.1.**1a**: Motion range in anatomical specimens (only ligaments remaining)

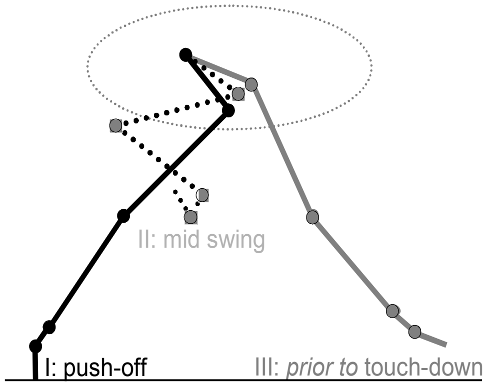

Fig. 4.2.1.**1b**: Motion range in live ostrich running (50 kmh^{-1}, obtained from Grzimek & Grzimek, 1959)

Discussion and conclusions

Motion range of pelvic limb joints is constrained by the interplay of joint surfaces and ligaments

This investigation revealed that the range of motion among leg segments is near-identical in both anatomical and live specimens in regard to maximum extension values of knee, intertarsal and metatarsophalangeal joint. This consistency persisted even after all muscles were removed with only ligaments remaining in the kinematic chain, indicating that ostrich hind limb dynamics are managed to a significant degree by passive elements that ensure a controlled swing-plane with minimal deviation.

Since the excursion angles of knee, intertarsal and metatarsophalangeal joint are greater in running compared to walking, it can be expected that this trend persists into higher velocities as speed and stride length are generally coupled. This increased excursion angle would necessarily include the hip joint as indicated in the study by Gatesy & Biewener (1991).

Although not quantified in the present study, it has been shown that the ligamentous system also guides limb joints through the mediolateral rotation range. When standing and during stance phase in locomotion, overall limb posture must be adjusted to uneven substrate, inclines/declines or other external factors to maintain balance and stability. Adjustments to posture are predominantly achieved by the knee joint (e.g. Stolpe, 1932, Fuss & Gasser, 1992; Rubenson et al., 2007) which exhibits the comparatively greatest range of inherent rotation since mediolateral rotation is rather restricted at the hip joint (Firbas & Zweymüller, 1971) and the distal joints (Chapters 4.2.2 & 5). The knee is located quite proximally to the Centre of Mass/trunk of the animal (Chapter 4.1.3) and at the same time acts primarily on the proximal starting point of the swinging part of the limb. Furthermore, the ostrich knee joint is located at the end of a relatively short femur (Chapter 4.1.3) thus combining a useful adjustment apparatus with the benefits derived from a short, highly-muscled lever (Chapters 4.1.1 & 4.1.2).

In summary, passive limitations to degrees of freedom provide substantial benefits in energy management to economise locomotion but an overly stiff limb may be disadvantageous due to undesirable reductions in overall articulation and mobility. The ostrich has balanced this conundrum by establishing a limb in which articulations are constructed more by form closure than force closure (Bögelsack et al., 2000), wherein extremely coherent joints provide the minimum degree of rotation required to allow adjustments in overall limb position to achieve direction changes and adjustments for ground conditions. Manoeuvrability is achieved by adjusting the degree of flexion in the knee joint in particular, within an overall system of limb articulation that increases the range of mediolateral and internal/external rotation of all joints in relation to degree of flexion. Therefore, increased joint flexion allows increased mediolateral and internal/external rotation as verified by Rubenson et al. (2007) in their study with over-ground running ostriches where rotation of distal joints is minimal during stance phase. This arrangement is similar to humans where rotation of the extended knee during standing is not possible thus enhancing columnar support of the leg. When extreme changes in direction are required at higher speeds, the ostrich will use the aerodynamic potential of its large wings to navigate terrain (Chapter 4.3.1).

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4.2.2 The intertarsal joint of the ostrich (*Struthio camelus*): Anatomical examination and function of passive structures in locomotion

The ostrich (*Struthio camelus*), the largest extant bird, is a highly cursorial animal and is acknowledged as the fastest biped with the greatest capacity for long-endurance running (Alexander et al., 1979; del Hoyo et al., 1992; Grzimek & Grzimek, 1959; Hallam, 1992). As an inhabitant of the African savannah and steppe, the ostrich relies on its migratory abilities to cover great distances. Generally, adult feral ostriches use 60% of daylight time walking and travelling while occupying territories in excess of 25 km², 20 to 33% of the day foraging and an additional 16% of time standing (Bertram, 1992; Williams et al., 1993). With a life expectancy up to 85 years, ostriches spend a significant amount of time on their legs and a specialised locomotor system can be expected.

In this context it is not surprising that the musculoskeletal morphology of *Struthio*´s pelvic limb has been the subject matter of various studies (e.g. Abourachid & Renous, 2001; Alexander et al., 1979; Bezuidenhout, 1999; Glutz von Blotzheim, 1958; Gadow, 1880; Gangl et al., 2004; Haughton, 1865; Liswaniso, 1996; Mellet, 1985; Pavaux & Lignereux, 1995; Sales, 1996; Schaller et al., 2005; Smith et al., 2006; Stolpe, 1932; Wagner, 2004; van den Berge et al., 1993; Weissengruber et al., 2002). In addition to predictably high muscle-power output (Smith et al., 2006), *Struthio*'s pelvic limb possesses a multi-jointed system consisting of interconnected bi- and triarticular muscles in which excursion of knee and all distal joints is mandatorily coupled with controlled abduction of the 4th toe (Schaller et al., 2007; Weissengruber et al., 2003). When compared to other cursorial ratites, muscle mass in the ostrich leg is the most proximally concentrated at the pelvis and relatively short femur while the distal leg segments, worked *via* long tendons, are comparatively the lightest and most elongated to provide a large action radius (Schaller et al., 2005). A further increase of distal limb segment length is achieved by permanent elevation of the metatarsophalangeal joint above the ground plane. This unique supra-jointed toe-posture likely increases elastic energy storage and provides shock absorption during fast locomotion (Rubenson et al., 2007; Schaller et al., 2005). As the only extant didactyle bird, the mass of the distal limb is further minimised by the absence of the second toe and its associated muscles (Hallam, 1992). Structurally, the interacetabular distance is relatively the smallest amongst all bird species, resulting in narrow guidance of limb motion at the hip joint (Firbas & Zweymüller, 1971).

Although the musculoskeletal system clearly drives limb motion, it is not the only potent constituent of the locomotor apparatus. Ligaments, menisci, cartilage and their interactions with skeletal anatomy play a vital role in all stages of locomotion. The importance of this passive locomotor system has been discussed in only a limited number of studies where constraints to joint movement and their possible influence on the dynamics of ostrich locomotion have been addressed (Bell, 1847; Fuss, 1996; Gangl, 2001; Hertel & Campbell, 2007; Langer, 1859; Stolpe, 1932; Weissengruber et al., 2003). The significance of ligaments in avian species is further demonstrated by a study about a pectoral ligament mechanism and its role in the evolution of flight (Baier et al., 2006).

The intertarsal joint is composed of distal tibiotarsus and proximal tarsometatarsus and, due to the similar lengths of tibiotarsus and tarsometatarsus, is located nearly at the vertical midpoint of the slender, elongated distal limb in large ratites (e.g. Alexander, 1983).

As typical for avian species, the knee and hip joint are flexed during ground contact as a result of the horizontally positioned femur while the intertarsal joint remains in a predominantly extended state to provide columnar support for the trunk mass – similar to the extended knee joint in standing humans (e.g. Gatesy & Biewener, 1991; Kummer, 1956; Stolpe, 1932).

The intertarsal joint is distinct from the more proximal hip and knee joint due to the absence of encapsulating musculature. Passive structures like ligaments, in combination with the morphology of joint surfaces, presumably play a dominant role in the stabilisation and guidance of this joint. Functional morphological evidence of the importance of these passive structures has been presented for the human knee (e.g. Muller, 1993 a, b).

The present study describes the prominent ligamentous system of the intertarsal joint and its interactions with joint surfaces and protrusions to determine the role of these structures in ostrich locomotion.

In the course of our preliminary manual manipulation experiments with intact distal limbs (tibiotarsus, tarsometatarsus and phalanges) of eight ostriches, a significant resistance occurred when flexing the intertarsal joint from a fully extended position. Moreover, with the tibiotarsus held immobile, the tarsometatarsus automatically snapped back towards full extension if released when the intertarsal joint was not flexed beyond a point of seemingly highest resistance. If flexed beyond this angle, resistance gradually decreased to a point where the limb automatically snapped towards flexion. We refer to this effect as the engage-disengage mechanism (EDM) where the “engaged” state represents intertarsal joint angles that automatically return to full extension and the “disengaged” state refers to angles of flexion attained after overcoming the point of highest resistance resulting in relative freedom of movement in the tarsometatarsus. This is a bi-directional effect with a similar, but less pronounced, resistance encountered when moving the limb from flexion towards extension. The effect remained evident after removal of all muscles and their corresponding tendons, indicating that this joint behaviour is entirely intrinsic to joint anatomy. A related mechanism has been identified in the elbow and ankle of various large mammals where it provides some passive support in the standing posture (e.g. Hildebrand, 1995; Hultkrantz, 1897; Nickel et al., 2006). Bell (1847) and Langer (1859) describe a “Schnappbewegung“ (snapping motion) in the hind limb of herons and large ratites. However, Stolpe (1932) refers to Langer’s study in his monograph about avian hind limb function and could not validate snapping actions in the intertarsal joint of his ratite specimens. Hence, a parallel aim of this study was to document the existence of this mechanism and provide a detailed anatomical description of its components. In order to explore functional implications for locomotion in live ostriches, we designed a method to yield first-time quantification of the EDM's inherent resisting forces in anatomical specimens and subsequently correlate these data with live kinematics of over-ground walking and running ostriches.

Materials and methods

Macroscopic dissection of the intertarsal joint and quantification of joint moments

The anatomical material used in this analysis was obtained from freshly slaughtered adult ostriches from a local ostrich breeding facility. The birds had a slaughter weight of 90 – 100 kg and were kept in accordance with regulations of German law for ostrich farming. First, maximum flexion and extension angles of the intertarsal joint were measured. Subsequently, the skin of tibiotarsus and all tibiotarsal muscles were completely removed with only the ligaments and cartilaginous structures remaining. The limb was again manipulated and measured to determine the extent to which ligaments and cartilage, as passive structures, guide motion. Manual manipulations with and without the Cartilago tibialis, a cartilaginous structure encasing the caudal intertarsal joint surface and providing a pathway for the tendons of toe flexor muscles, had no effect on joint and ligament function (i.e. EDM effect, ligament orientation during motion). As the presence or absence of the Cartilago tibialis did not alter joint function and obscured the caudal section of the intertarsal joint, it was removed to make the caudal joint elements visible. The origin and pathways of passive structures of the intertarsal joint were then identified and positional relationships throughout the range of motion were recorded on digital video (Canon MV 550i and Konica KD-500Z) to allow frame-by-frame analysis of joint articulations. Passive (i.e. non-muscular) moments resisting flexion and extension in the intertarsal joint were measured in isolated limbs (sub-knee preparations; **Fig.** 4.2.2.**1**). The skin, muscles and corresponding tendons were removed from the tibiotarsus and the intertarsal joint while tarsometatarsus and toes remained intact (total mass: 2.7 kg; tarsometatarsal length: 0.46 m). Measurements were performed with each limb in two different configurations.

In the first experiment, the prepared limb was oriented horizontally on a dissection table with the tibiotarsus raised above grade and fixed to the table to allow the tarsometatarsus to move freely in a horizontal plane through flexion and extension during manual manipulation.

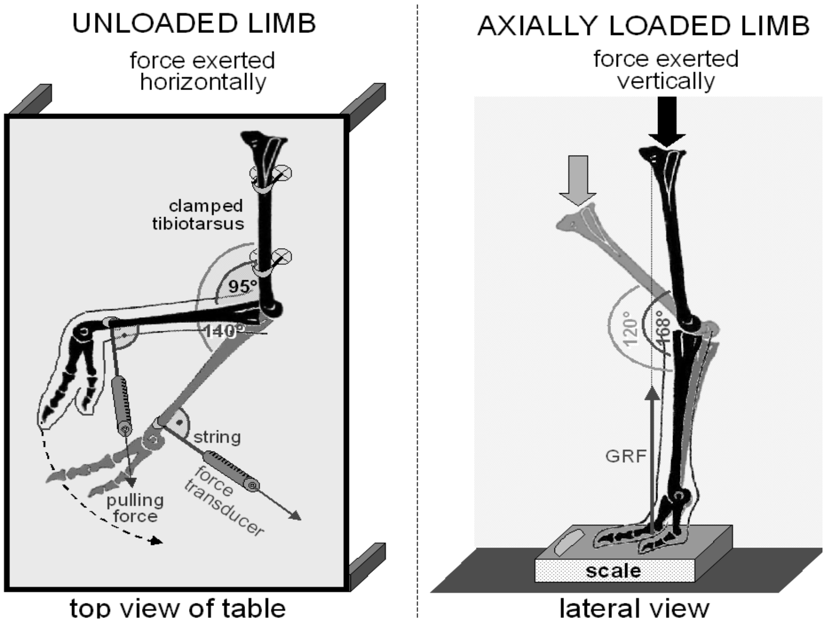


Fig. 4.2.2.**1:** Experimental set-up for quantification of joint moments with the distal limb (tibiotarsus, tarsometatarsus, toes) unloaded (left) and axially loaded (right).

A calibrated mechanical force transducer (100 N max) was attached to the distal end of the tarsometatarsus using a 15 cm non-elastic string. Throughout the experiment, a machinist's square was used to maintain the force transducer in a position perpendicular to the long axis of the tarsometatarsus. Forces were measured while pulling the tarsometatarsus slowly towards flexion and extension (approximately 1°/s; inertial effects negligible). Multiplying these forces by the distance to the intertarsal joint centre yields the moment required to overcome the resistance in the joint against pure rotation (without axial loading of the joint) imposed by passive joint structures only (without gravitational or inertial effects). The opposite of this moment is the passive resistive unloaded moment.

Experiments were filmed with a digital camera (Canon MV 900, 50 frames/s) and measured forces were vocally reported simultaneously (approximately one reading/1°) on the audio channel. Afterwards, the angular displacements of the tarsometatarsus with respect to the tibiotarsus were accurately calculated from the digitised video frames (Didge, Alistair Cullum, Creighton University, Omaha, USA) and were combined with the recorded moments.

In the second experiment, the preparation was oriented in an *in vivo* standing position with the toes on a digital scale (100g calibration, **Fig. 4.**2.2.**1**). With the intertarsal joint fully extended (i.e. the ‘engaged’ position as described in the introduction), a manual downward pushing force was gradually increased on the proximal tibiotarsus in order to overcome the resistance of the engaged joint to drive the intertarsal joint slowly (about 1°/s) into flexion. Movements were videotaped in lateral view as in the former experiments. A second camera (Canon MV 500i, 50 frames/s) was used to simultaneously record the scale reading. Digitisation of the lateral views (cf. above) provided positional information of the limb segments. These data, combined with the recorded scale readings (i.e. vertical forces), were used to calculate static equilibrium. In a first step, the entire preparation was considered a free body in order to obtain the orientation and magnitude of the pushing forces at the tibiotarsus. Next, the equilibrium of the limb segments could be calculated, yielding, amongst other data, the passive resistive moment of the axially loaded intertarsal joint. Measurements were carried out immediately after slaughter in order to avoid any effect of tissue decay. Manual pulling experiments were carried out three times each by two experimenters. Averages of these measurements were used in final calculations.

Data acquisition of joint motion range in live ostriches

The live ostriches used in this study were hand-raised from 10 weeks of age to present day in an outdoor-enclosure (6400 m²) near Heidelberg, Germany. Water was available *ad lib.* with daily feedings of special ostrich feed dependant on freely available pasturage. The living conditions and enclosure were maintained in accordance with German ostrich raising standards. To habituate the ostriches to the experimental set-up, they were allowed access to the sampling corridor for increasing periods of time starting eight weeks in advance of data capture.

To determine excursion angles of the intertarsal joint in live ostriches, kinematic data for walking to intermediate running speeds ranging from 0.5 ms^{-1} to 3.5 ms^{-1} was obtained. Experiments were carried out with two 3-year-old females (90 kg) and one 13-year-old male (140 kg) in a level-ground corridor (76 m long & 3 m wide) which was separated from the main outdoor enclosure by coarse wire mesh.

Fig. 4.2.2.**2**: Ostrich with joint markers. Left lateral view.

Knee, intertarsal and metatarsophalangeal joints were marked as indicated in **Fig.** 4.2.2.**2** by applying locator marks (4 cm in diameter) with ALUNIC aluminium spray commonly used in animal healthcare as a disinfectant. This spray is clearly visible on film and cannot be removed by the ostriches. Two digital video cameras (Canon MV 500i & 900, 50 frames/s) were oriented at a 90° angle to simultaneously capture front/back and lateral view. The cameras were installed at a distance of 5 m from the focal zone through which the ostriches passed, and were synchronised using on-screen time-code.

At least two complete stride cycles were recorded at each pass. Only walks and runs that remained straight for at least three stride cycles were included in the data pool, as verified by the front/rear view camera. Five straight walks (duty factor: ~ 0.65; ~1 ms^{-1}) and five straight runs (duty factor: ~ 0.5: 3 – 3.5 ms^{-1}) were selected for analysis. Movements of the following anatomical points were digitised frame-by-frame (Didge, Alistair Cullum, Creighton University, Omaha, USA): lateral knee joint, intertarsal joint, metatarsophalangeal joint.

Results

Anatomical description

The anatomical terminology used in the following descriptions concur with the Nomina anatomica avium (Baumel et al., 1993). On the lateral side, the ligamentous system of the intertarsal joint consists of one ligament, a reduced muscle and two ligaments on the medial side. A central Ligamentum anticum as found in many bird species is missing. While fully developed in many avian species, the M. fibularis brevis (MFB) in *Struthio* is reduced to a tendon and essentially functions as a ligament. The tibiotarsal attachment of the MFB is located distolaterally below the end of the fibula (**Fig.** 4.2.2.**3, B & C**). In the fully extended joint, the MFB runs transversally, crossing the origin of the Ligamentum collaterale laterale, and inserts proximolaterally at the plantar surface of the tarsometatarsus. The origin of the Ligamentum collaterale laterale (LCL) lies in the Depressio epicondylaris lateralis (**Fig.** 4.2.2.**3, A)**. Because of the funnel-shaped form of the Depressio, the area of origin of the LCL is very localised and concentrated. In its course, the LCL broadens and attaches to the tarsometatarsus cranioproximally at the Impressio ligamentum collaterale laterale. In a full course from extension to flexion, the MFB traverses the LCL with ligaments crossed at full flexion (**Fig.** 4.2.2.**3, C**).

On the medial side, the Ligamentum collaterale mediale (LCM), similar to the lateral LCL, originates in the Depressio epicondylaris medialis of the distal tibiotarsus, broadens, and after a straight course inserts proximomedially at the tarsometatarsus (**Fig.** 4.2.2.**3, E**). Caudally to the LCM runs the prominent Ligamentum collaterale mediale longum (long LCM). It originates at a distinct triangular attachment on the distal tibiotarsus (**Fig.** 4.2.2.**3, D**). In the extended joint, this ligament is oriented distally parallel to the LCM (**Fig.** 4.2.2.**3, E**) and inserts at the proximomedial tarsometatarsus (**Fig.** 4.2.2.**3, F)**.

Table 4.2.2.**1: Identification of ligamentous structures and osseous protrusions**

structure	**origin**	**insertion**	**position**	**length at full ext.**
M. fibularis brevis, tendonous (MFB)	On tibiotarsus (Tib.) distally at end of fibula	Proximolaterally on plantar surface of tarsometatarsus (Tmt.)	Medially of Tendo lateralis of M. fibularis longus	7.5 cm
Lig. collaterale laterale (LCL)	Depressio epicondylaris lateralis (DEL) of distolateral Tib.	Cranially at Impressio lig. coll. lat. of proximal Tmt.	Medially of M. fibularis brevis	4 cm
Meniscus lateralis (ML)	On proximolateral tarsometatarsal joint surface	At medioventral tarsometatarsal joint surface	C-shaped at lateral tarsom. joint surface	
Lig. collaterale mediale longum (LCML)	Triangular attachment at lateral distomedial tibiotarsus	At proximomedial tarsometatarsus	Caudal of LCM	26 cm
Lig. collaterale mediale (LCM)	Depressio epicondylaris medialis (DEM) of distomedial Tib.	Craniomedial at Impressio lig. col. lat. of proximal Tmt.	Medially of LCML	4 cm
Epicondylus medialis (EM)			Distomedial tibiotarsus	
Cranial crest (c1)			Cranial rim of Condylus lateralis	
Central crest (c2)			Central rim of Condylus medialis	
Osseous protrusion (S)			Distocaudally at medial tibiotarsal condyle	

The entire length of the LCML amounts to 26 cm but is fused with the tibiotarsus for 4 cm and with the first two-thirds of the tarsometatarsus for 15 cm. The unattached 7 cm segment interacts with the medial epicondyle which acts as an arresting barrier for the LCML towards flexion as explained in more detail below. This segment is connected to a broad ligament originating from the joint capsule at the Depressio epicondylaris medialis (**Fig.** 4.2.2.**3, F**). As opposed to the ligaments on the lateral side, LCML and LCM do not cross each other during a full course from extension to flexion (**Fig.** 4.2.2.**3, F**).

Many bird species possess two menisci while the ostrich has only one C-shaped meniscus located at the lateral tarsometatarsal joint surface (**Fig.** 4.2.2.**3, H**). The meniscus is composed of a cartilaginous Cornu craniale and Cornu caudale (**Fig.** 4.2.2.**3, H**) and connects to the Ligg. collaterale laterale and mediale and to the Cartilago tibialis *via* small ligaments (**Fig.** 4.2.2.**3, G**). During a motion cycle, all intertarsal ligaments are deflected by 1) vaulted contours situated on the lateral joint rim (cranial & central crest, **Fig.** 4.2.2.**3, B & C**) and 2) medially by the protruding Epicondylus medialis (**Fig.** 4.2.2.**3, D, E & F**).

For the upcoming functional description it is important to note that the Epicondylus medialis has a plateaued surface contour. While less evident in macerated bone samples, osseous protrusions gain additional height and contour with hyaline cartilage intact as shown in the fresh specimens used in this study.

Fig. 4.2.2.**3**: Anatomical photo reference in accordance with **Table** 4.2.2.**1**

LATERAL VIEW

cranial **caudal**

proximal

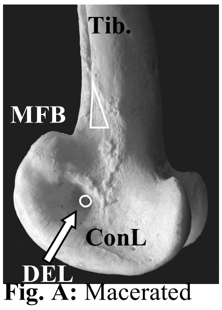


Fig. A: Macerated distal Tib.; LCL attachment = circle, MFB attachment = triangle, ConL = lateral condyle

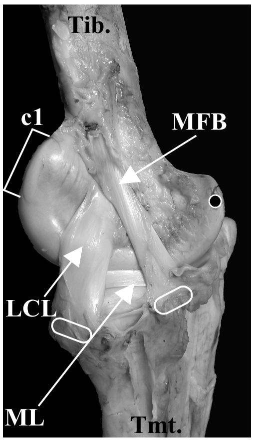
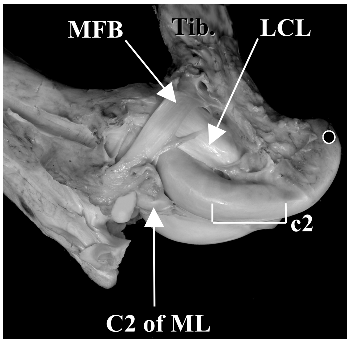


Fig. B: Intertarsal joint at maximum extension, attachment of LCL = left ellipse, attachment of MFB = right ellipse

Fig. C: Intertarsal joint in flexion, black dot indicates reference point



distal

MEDIAL VIEW

caudal **cranial**

proximal

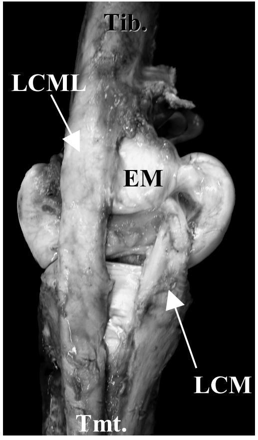


Fig. E: Intertarsal joint at maximum extension

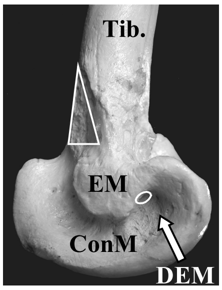


Fig. D: Macerated distal Tib.; LCM attachment = ellipse, LCML attachment = triangle, ConM = medial condyle

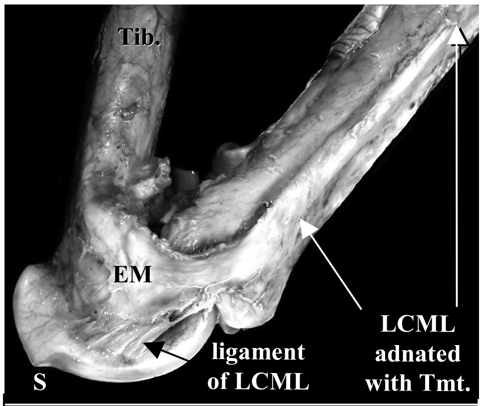


Fig. F: Intertarsal joint in flexion with osseous protrusion (S) to prevent hyper-extension and tensed laminar ligament preventing LCML from sliding over EM

distal

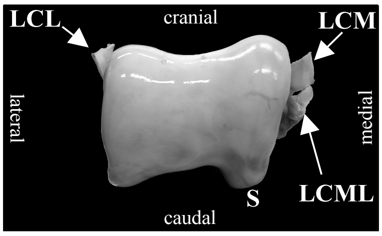


Fig. G: Tibiotarsal joint surface with LCL, LCM & LCML cut

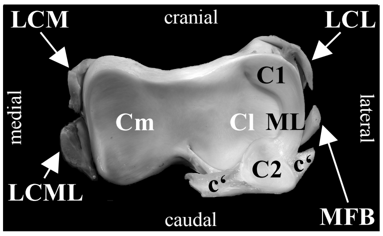


Fig. H: Tarsometatarsal joint surface with LCL, MFB, LCM & LCML cut, lateral meniscus (ML) with Cornu craniale (C1), Cornu caudale (C2) and assoiciated ligaments (c'); Cotyla lateralis (Cl) & C. medialis (Cm)

Functional description

Before describing the ligamentous system during a motion cycle including the expression of the engage-disengage mechanism (EDM), it should be mentioned that the intertarsal joint is not a simple hinge joint. It is a roll-and-glide joint which, in response to the contours of the joint surfaces, leads to external rotation of the tarsometatarsus where flexion is automatically coupled with tarsometatarsal abduction in the lateromedial (transverse) plane (max. 15°) and extension causes tarsometatarsal re-adduction. With the joint fully extended, tibiotarsus and tarsometatarsus form a straight axis from the frontal view. In this position, the intertarsal joint cannot be lateromedially rotated and exhibits a stiff condition.

The intertarsal joint maximum flexion angle in an intact anatomical specimen is 20° and maximum extension angle is 168°. The maximum flexion angle in a specimen with skin, muscles and tendons removed was 10° and maximum extension angle remained at 168°. The difference between maximum flexion angles is explained by the removal of the musculature acting as a physical barrier to further flexion in the intact limb.

Analysis of sequence of flexion

168°

At maximum extension (**Fig.** 4.2.2.**4**) the intertarsal joint is in an engaged position under the conditions of the EDM. With the tibiotarsus held immobile, force has to be exerted in order to overcome resistance and move the tarsometatarsus towards joint flexion. In addition, when flexing the joint up to 130° by moving the tarsometatarsus and subsequently releasing it, the tarsometatarsus rapidly snaps back to the maximally extended joint position. At maximum extension, the LCML rests caudally of the medial epicondyle and, like the other three ligaments, is in a tensed state. Lateromedial rotation is not possible in this position.

Over-extension of the intertarsal joint beyond 168° is not possible due to a triangular-shaped process on the medial condyle of the distal tibiotarsus. In combination with the corresponding caudal rim of the tarsometatarsal joint surface, this osseous process functions as a structural limiter to the maximum angle of extension when all ligaments are intact (**S in Fig.** 4.2.2.**3, F & G**). On the lateral side, the thickened Cornu caudale of the meniscus completes this over-extension barrier (**Fig.** 4.2.2.**3, H**).

140°

At this flexion angle, the tarsometatarsus has begun to rotate outwards. On the lateral side of the joint, the MFB runs over the condylar crest that protrudes further into the sagittal axis due to the outward rotation of the joint. As a result, the tendinous MFB remains tensed despite a virtually shortened distance between origin and insertion areas (**Fig.** 4.2.2.**4**). Simultaneously, the MFB begins to interact with the LCL, further affecting the tension of the MFB.

On the medial side of the joint, the medial epicondyle is now situated beneath the LCML. Comparable to the lateral side, the tension of this ligament is maintained by a protrusion, in this case the epicondyle, despite the shortened distance between areas of insertion.

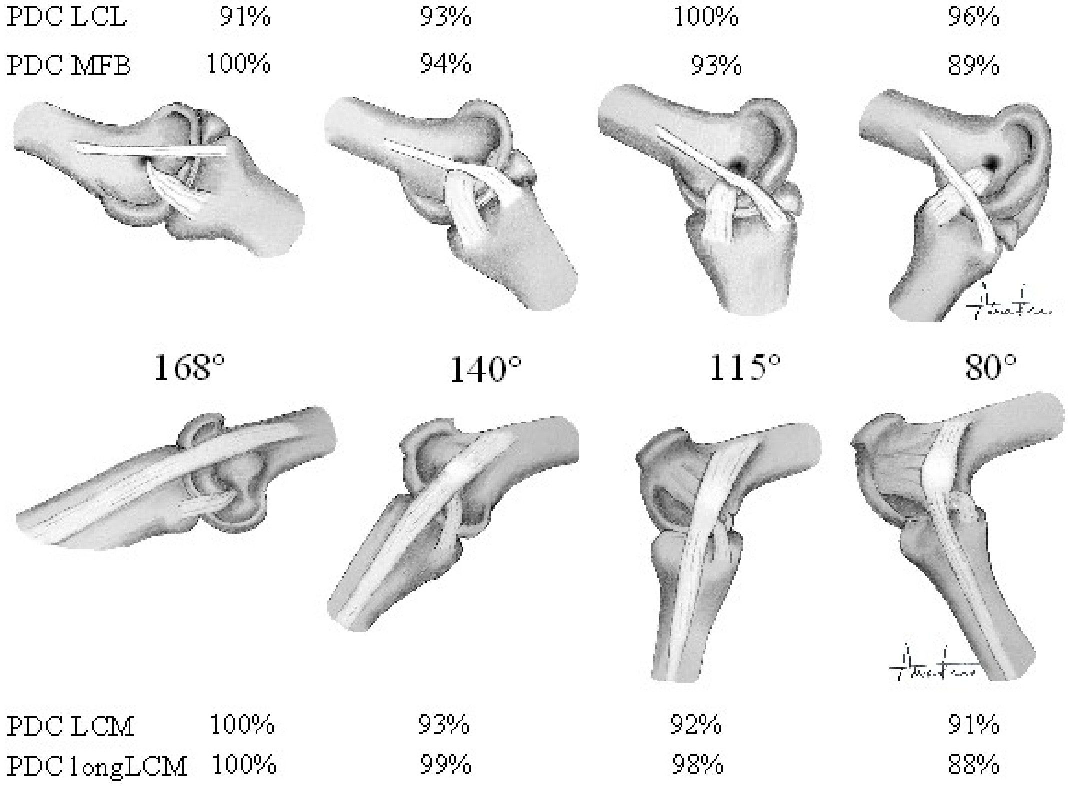


Fig. 4.2.2.**4:** Ligament interactions with osseous protrusions in the course of flexion.
Lateral view above, medial view below; PDC = Percentage distance change of ligament attachments; Cranial crest clearly visible at lateral view at 168° and central crest at 80°.

120° +/-5°

In this range of excursion, the joint is in a state of transition. In manual manipulations, releasing the tarsometatarsus results in rapid movement of the joint to either a flexed or extended position. This automatic transitional effect can be explained by the particular ligament arrangement at this stage where the LCML on the medial side is positioned on top of its corresponding epicondyle while on the lateral side the MFB is positioned at the apex of its corresponding central crest. As a result, these ligaments are simultaneously in a maximum state of tension. To resolve these high tensile stresses, the relative angle of tibiotarsus to tarsometatarsus automatically shifts to allow the MFB to descend its crest while, in the course of flexion, the areas of origin and insertion of the LCML move closer together and ligament stress is reduced. During the transition at 125°–115°, the two overlapping lateral ligaments (LCL and MFB) form an "X-orientation", with the intersection of the X located directly at the interface of the intertarsal joint space and horizontally opposed to the medially originating forces generated by the LCML/epicondyle interaction. This X-orientation is possible because the point of origin of the MFB is located further proximodorsally to that of the LCL and consequently travels in an arc around the origin of the LCL (black dot in **Fig.** 4.2.2.**3, B & C**).

115° (transition point of the engage-disengage mechanism)

At this critical angle, the LCML covers the plateaued surface of the medial epicondyle completely and the broad connective ligament between condylar rim and LCML begins to stretch. On the lateral side of the joint, the MFB has moved past the central condylar crest and tension is reduced. However, LCL and medial LCM remain stretched over their respective condylar rim. When the tarsometatarsus is released in this position, it rapidly snaps towards either flexion or extension depending on a prevailing external force.

80°

The MFB, now fully overlapping the LCL, is in a state of lesser tension. On the medial side, the broad connective ligament between condylar rim and LCML is clearly stretched. This ligament does not restrict further flexion but rather anchors the LCML against traversing the epicondyle completely where it would be “trapped” on the cranial side of the joint.

As opposed to the longer MFB and LCML, the LCL and LCM undergo less distortion during a full excursion cycle with smaller changes to the virtual distance between their areas of attachment and remain tensed throughout the range of motion. This is facilitated by i) the inherent joint mechanics wherein the cranial tarsometatarsal joint surface glides/rolls along the cranial tibiotarsal joint surface allowing the distances between ligament attachment areas on both sides of the cranial joint to remain rather constant ii) the swivel nature of the punctiform areas of origin of LCL and LCM in their respective depresii at the distal tibiotarsus to allow a wide arc of mobility and rotation without detrimental stress at the points of ligament insertion and iii) ligament insertion origins that concur with the centre of rotation of the intertarsal joint to prevent dislocation of the tibiotarsal attachment during the motion cycle. These two anatomically similar ligaments provide stabilisation of the mediocranial connection between proximal tarsometatarsus and distal tibiotarsus throughout the entire articular range.

In addition to their role in the EDM, the LCML and MFB provide a critical guiding function in joint mechanics. This became obvious in anatomical specimens where ligaments were cut after experiments were concluded, and only LCL and LCM remained intact. When fully extended, the joint surfaces still appeared coherent and ab-/adduction or rotation were greatly limited, but increasing degrees of flexion caused a gap to occur between the dorsal joint surfaces and the tarsometatarsus was no longer bound to its arc of motion. Cutting either the medial LCML or the lateral MFB – while leaving the respective counteracting ligament intact – completely eliminated the effects of engagement and disengagement.

When re-extending the intact joint the lateral MFB and the LCL essentially reverse their interplay sequence as described for flexion, except that resistance encountered by the MFB is provided by the comparatively less prominent cranial condylar crest. The maximum resistance against extension occurs at 95°.

Medially, the sequence is simply reversed with the LCML starting its descent from the epicondyle at 140°. As above, the tarsometatarsus will snap towards flexion or extension depending on the joint angle at point of release within a transitional range from 105° - 115°.

During articulation, the meniscus compensates for the incongruent joint surfaces and ensures joint surface closure. This is important because the lateral joint socket is rather flat with the meniscus providing coherence for proper joint articulation.

In summary, manual manipulations of the intertarsal joint have identified three distinct stages during joint articulation. In the extended position (stance default angles of 168° through to 140°), the joint is in an engaged condition where resistance increases as the joint is flexed towards the transition stage. During the transition stage (125° to 105°) resistance has been overcome and the joint exhibits a balanced but volatile condition with maximally tensed ligaments (~ 115°) that is resolved by rapid movement towards either flexion or extension. In the flexed position (95° to 20°), the joint is in a disengaged state where resistance is increased as the joint is extended back towards the transition stage.

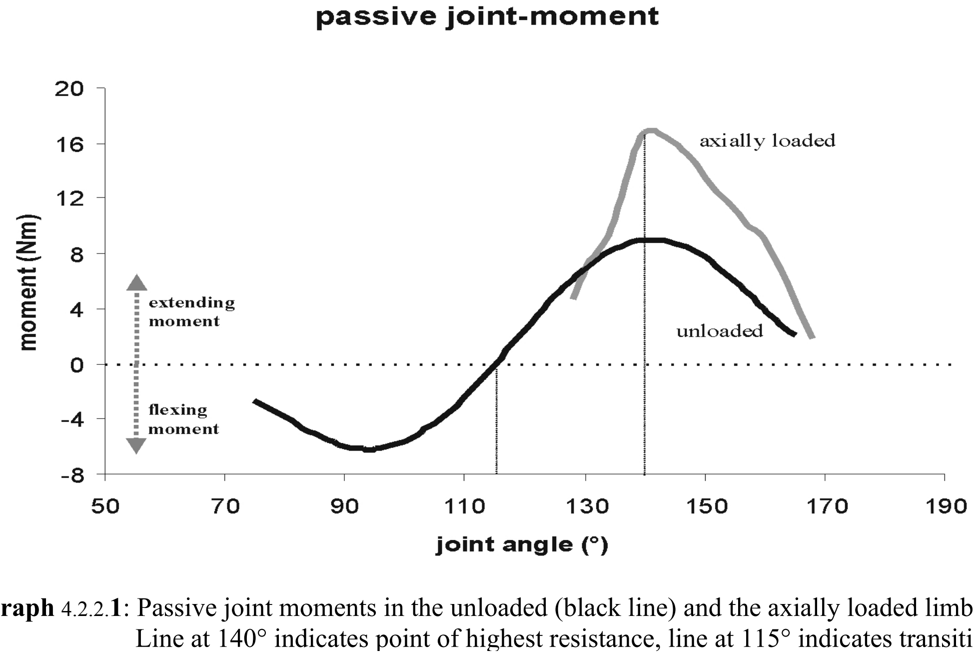
Quantification: Passive moments of the intertarsal joint

1) Resistance against flexion and extension: the unloaded joint

Graph 4.2.2.**1** presents the results of the measurements with the limb in the horizontal plane (see **Fig.** 4.2.2.**1*)*.** Starting from full extension, the resistive moment builds up gradually to become maximal (9 Nm) at a flexion angle of 140°. When flexed further, the resistance against flexion decreases, falling to 0 Nm at 115°. Beyond this angle, passive joint moments become flexing moments and the tarsometatarsus snaps rapidly towards maximum flexion. During manipulation towards extension, a similar but opposite passive behaviour of the joint was observed. Resistance against extension grew to a maximum of about 6 Nm at 95° and decreased as it transitioned into an extending moment when crossing the 115° boundary.

2) Resistance against flexion: axial loading in the standing limb

As in the experiment with the unloaded limb, the moment at maximum extension is 2 Nm with the highest values against flexion (18 Nm) occurring at a 140° angle. When compared to the horizontally oriented limb (unloaded), the moments in the loaded limb at peak are twice as high in value. However, the transition point remains consistent at 115° where no resistance is encountered (**Graph** 4.2.2.**1**).



Graph 4.2.2.**1**: Passive joint moments in the unloaded (black line) and the axially loaded limb (grey line). Line at 140° indicates point of highest resistance, line at 115° indicates transition point.

3) Resistance against extension in vertically oriented suspended limb

(not depicted in **Graph** 4.2.2.**1**)

Once full flexion had been attained and phalanges were suspended above the scale the intertarsal joint assumes a default flexed angle of 95° with tibiotarsus held and positioned vertically. This angle corresponds to the point of maximum resistance against flexion in the horizontal unloaded limb. A rapid upwards pulling at the proximal end of the tibiotarsus was sufficient to overcome this resistance and the intertarsal joint quickly engaged towards maximum extension.

Correlation of EDM with real-time kinematic data

Figure 4.2.2.**5 a & b** provides kinematic data for intertarsal joint excursion throughout one complete stride in walking (a) and running (b). This allows correlation of manual manipulation data with flexion/extension data in the live bird. This chart also superimposes the location of the EDM transition zone within the stride cycle (orange lines/areas). In accordance with data from manually manipulated hind limbs, the maximum extension angle of the intertarsal joint in walking and running is 168°. During the entire period of ground contact (indicated by black bracket/lines) in both walking and running the intertarsal joint remains nearly fully extended with flexion angles never below 164° and 160° respectively.

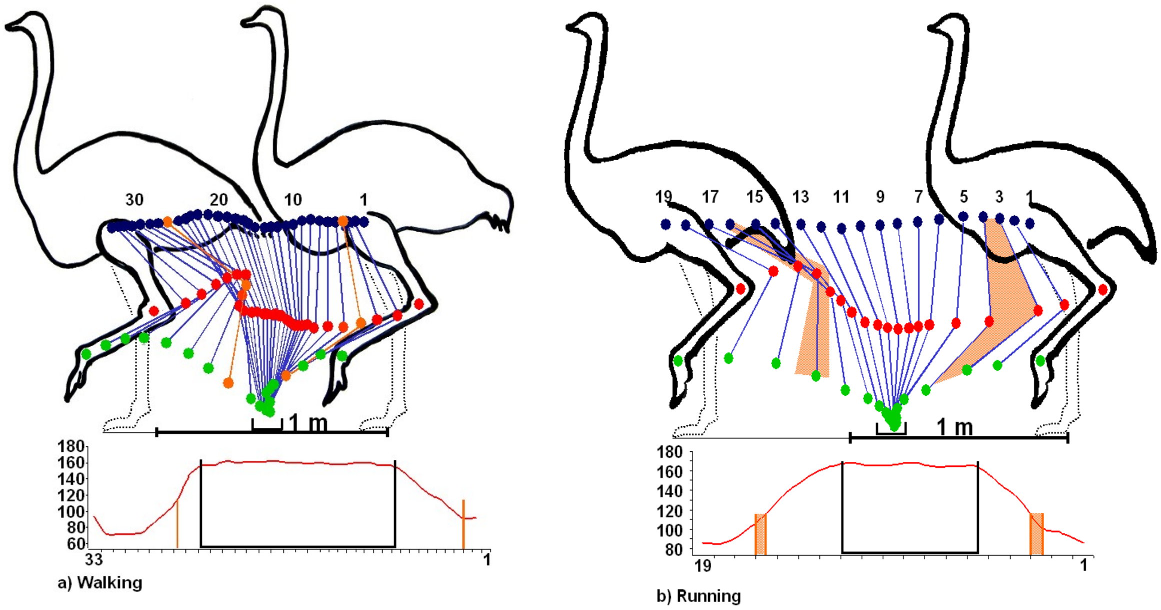


Fig. 4.2.2.**5 a & b:** Kinematic analysis of stride cycle and EDM in walking and running.
Blue points = knee joint, red points = intertarsal joint, green points = metatarsophalangeal joint. Orange lines/areas indicate the limb configuration where EDM transition occurs (either in extension before touch down or in flexion after toe off) during the swing phase of the stride cycle. One point/number represents one video frame (25 frames = 1 sec). The black brackets show the period of ground contact.
The corresponding graphs (bottom; not to same scale) show flexion/extension angles of the intertarsal joint over a full motion cycle; black brackets indicate ground contact time, orange lines/areas indicate EDM transition.

Although unable to gather first-hand data on ostriches running at high speed over ground, lateral view footage of feral ostriches in the Serengeti was used to estimate maximum flexion and extension angles of the intertarsal joint (Grzimek & Grzimek, 1959). This male adult ostrich was reported with a running speed of 16.4 ms^{-1} (60 kmh^{-1}). Maximum flexion reached 45° during the mid-swing phase and maximum extension (168°) was observed during stance phase. Maximum flexion during ground contact occurred at mid-stance phase and was measured at 140°. This indicates that the point of highest resistance against flexion as determined in the experiments (i.e. 140°) is only achieved during high-speed running and further establishes that the EDM is in the engaged state during all stages of ground contact.

In walking, an abrupt upward vertical trajectory of the intertarsal joint occurs after toe-off. This coincides with the exact angle at which the intertarsal joint disengages towards flexion when releasing the tarsometatarsus in the experiment with loaded and unloaded limbs (see above). In running, a forward thrust of the intertarsal joint occurs just prior to touch down in the course of joint extension. This effect also coincides with the joint angle at which the mechanism engages as described in the experiments performed with anatomical specimens (see above). Given these results, it can be accepted that the transition point of the EDM as qualified in anatomical specimens exists in the live animal during locomotion.

Discussion

In this study, the *bauplan* of the intertarsal joint of *Struthio* and possible *in vivo* effects of the EDM were investigated by combining data obtained using anatomical and kinematic methodologies. The results showed that the ligaments of the intertarsal joint serve four interdependent functions. Firstly, they achieve a characteristic stabilisation of joint surfaces relative to one another and provide the requisite tension in combination with the lateral meniscus to maintain joint coherence in the absence of direct muscle control. Secondly, they guide motion of the tarsometatarsus through flexion and extension in concert with joint surface contours. Thirdly, the ligaments prevent hyperextension of the joint in combination with a distinctly shaped osseous protrusion located caudally at the medial tibiotarsal condyle and at the Os menisci laterale. Finally, the interplay of intertarsal ligaments with joint contours and protrusions form the basis for an engage-disengage mechanism that appears to support the extended joint position during stance phase and provide additional non-muscular dynamic impetus to the lower distal limb during swing phase.

Anatomical basis for passive intertarsal joint management

The reductive dissection showed that muscles, tendons and the intertarsal Cartilago tibialis are uninvolved in guidance of the intertarsal roll-and-glide joint through the full motion cycle, indicating that the ligamentous system interacts with the structures of the intertarsal joint within a self-contained system.

Ligament tension throughout the range of motion is maintained by the interplay of ligaments and their deflection by protrusions present in the hyaline cartilage of the tibiotarsal joint surface. The distinct locations of the two protruding lateral condylar crests are presumably related to the inherent outward rotation of the tarsometatarsus during flexion. The distance covered by the joint surfaces on the medial and lateral sides is not equal and likely requires compensation to maintain steady ligament tension.

Thus, the central crest counteracts towards flexion and the cranial crest counteracts towards extension when deflecting the LCL and MFB. The location and domed shape of these crests may provide a tension pre-load modulator to slope-up the stabilising properties of the lateral ligaments in advance of the major shear force that originates on the medial side as the LCML is increasingly tensed by the protruding epicondyle. This arrangement could ensure additional lateral joint stability prior to the EDM transition point of 115° in each direction, since the ligaments have not yet formed the stabilising X-orientation located directly at the lateral interface of the intertarsal joint space. This principle is also present in the avian knee where deflection of ligaments by protrusions leads to "a greater and lesser state of tension" but does not allow "distinct differentiation between a tensed and a relaxed state" (Fuss & Gasser, 1992). The constant state of tension of all intertarsal ligaments may also work in tandem with the elastic properties of the hyaline cartilage of the joint surfaces that compress somewhat under pressure. The exact extent of this effect should be studied further since the compliance of hyaline cartilage is commonly appreciated only in the context of shock absorption (Stolpe, 1932) but not considered in relation to ligament function.

The participation of the MFB in the intertarsal system is particularly interesting in that the actualised function of this tendinous muscle has, to our knowledge, not been previously clarified in the existing literature. While Pavaux & Lignereux (1995) termed it a second lateral ligament, Liswaniso (1996) described it as rudimentary and functionless while George & Berger (1966) erroneously declared it absent in all large extant ratites. In many avian species, where the MFB contains a venter, the tarsometatarsus can be rotated inwards (Stolpe, 1932). Since the ostrich exhibits only outward rotation, we assume that this led to the gradual reduction of this muscle's venter to its present form as an important ligament/tendon contributing to the engage-disengage mechanism. The MFB of the ostrich provides a good example of a structure whose function might be misinterpreted as rudimentary due to reduction but is, in fact, necessary for the gross functionality of the organism.

Presumably, the intertarsal ligaments also play an important role in acting against shear forces and support the fully developed M. fibularis longus, serving as a main extensor of the intertarsal joint (Gadow, 1880; Stolpe, 1932; Weissengruber et al., 2003). Due to its insertion at the proximolateral tarsometatarsus, it is the only muscle that acts directly on the lateral side of the intertarsal joint with its main end-tendon overlapping the MFB. An effective compensation against lateral and medial shear forces is especially important in running when body mass is accelerated and its impact on the joints at touchdown is drastically increased in comparison to walking.

To balance the incongruent joint surface of the distal tibiotarsus (**see Fig.** 4.2.2.**3, G & H**), the ostrich possesses a prominent Meniscus lateralis, which has been anatomically and histologically described by Stornelli et al. (2003) and Wagner (2004). Due to its connections with the tarsometatarsal joint surface and the lateral collateral ligament (LCL), the meniscus is automatically adjusted at each stage of joint motion with specific adjustment dependant on tarsometatarsal abduction/external rotation in the course of joint flexion. Stolpe (1932) further suggests function of the ossified Cornu caudale of the meniscus as an articular shock absorber in heavy *Struthio camelus* which corresponds to findings in the human knee where menisci have been found important for load transmission (Boyd & Myers, 2003).

A medial meniscus and central Ligamentum anticum, commonly present between the joint surfaces of many other bird species, e.g. chicken (*Gallus gallus*) and parrots (Psittaciformes), are missing at the tarsometatarsal joint surface of the ostrich. Since medial rotation of the tarsometatarsus does not occur in the ostrich, a medial meniscus is probably not required. The central Lig. anticum may have been fully reduced because it would hinder movement through the large flexion/extension radius required in the ostrich to achieve the large swing radius of the distal limb.

The LCML provides joint coherence during swing phase and significant support of the intertarsal joint during stance phase. The prominence of this major medial ligament is presumably linked to the mass and dimensions of the ostrich and counteracts shear forces during stance phase when the LCML is tensed in support of the extended joint. In analysis of skeletal material (Schaller et. al., 2005) all specimens of ostrich, emu, rhea and cassowary showed fissures associated with the LCML. The distal tibiotarsi of extinct moa skeletons (*Dinornis maximus*) also showed a deep 8 cm fissure for the LCML, as well as the protruding Epicondylus medialis that plays a major role in the EDM. In this biped of ~ 300 kg, we can expect that a stabilising mechanism of the intertarsal joint would have been helpful in supporting body mass on an extended distal limb. The smallest member of the ratite family, the New Zealand kiwi, does not feature the prominent scar of the LCML. It stands to reason that this chicken-sized bird (up to 3 kg) with its intertarsal joint permanently flexed during ground contact (Abourachid & Renous, 2000) would not require this stabilising mechanism.

To test whether body mass and limb posture might be correlated with structures associated with the EDM, the chicken (*Gallus gallus*; < 5 kg) was included in comparative skeletal analyses. Skeletal material did not show the tibiotarsal scars of the LCML and the Epicondylus medialis was of comparatively limited size and protruded less than in large ratites. In limb manipulation experiments with a fresh free-range chicken, no resistance during flexion or extension was detected and subsequent dissection confirmed the absence of the LCML.

This dissection also showed that the MFB was not reduced but featured a fully developed venter and, in the absence of elevated crests, its tendon slid freely over the distal lateral condyle of the tibiotarsus. This is common in the majority of avian species, which are much smaller and lighter than ratites and use legs and toes for complex actions not exclusively dedicated to terrestrial locomotion. In most birds the developed M. fibularis brevis supports tarsometatarsal control and manoeuvrability in the lower limb (Stolpe, 1932). Degrees of intertarsal flexion may be another crucial factor for reduction of the MFB and its integration in the ligamentous system. Many smaller bird species exhibit a flexed intertarsal joint during stance postures that might require the muscle control provided by a developed M. fibularis brevis. In contrast, large ratites use their vertically extended legs primarily for terrestrial locomotion in a planar environment. The reduction of a muscle intended for fine movement unnecessary to the ostrich presumably saves muscle mass and concentrates energy for limb motion in the fore-aft plane.

In summary, the morphology of intertarsal ligaments and joint surfaces in combination with condylar crests and contours of the medial epicondyle provide a coherent system of joint stability and motion range control. In addition, this joint complex provides the structural basis for the dynamic expression of an engage-disengage mechanism that may deliver locomotor benefits that exceed any associated metabolic cost.

Prior examinations of passive joint stabilising structures

The benefit of a passively stabilised intertarsal joint becomes apparent when considering that ostriches stand or walk very slowly for extended periods of time during foraging. With a trunk mass up to 100 kg perched on two long limbs, each with only two partly-elevated toes, the resulting small base of support presents a possible challenge to static stability. Maintaining standing position solely by muscle power for these long periods over a lifespan up to 85 years would be energetically disadvantageous. Anatomical features for economic stance postures are a common characteristic in the distal limb joints of larger quadrupedal cursorial mammals (e.g. Hildebrand, 1995). In the standing horse, the lower hind limb is locked by the quadriceps pulling the patella into a mating groove of the distal femur (e.g. Sack, 1989; Schuurman et al., 2003). In combination with the interplay of superficial digital flexor and calcaneus, the entire limb is locked using a four-bar system to allow near-effortless standing. Flexion of the knee unlocks the system and automatically flexes the ankle. But, as opposed to the horse, the two patellae (i.e. sesamoids) of the ostrich knee do not interact with a femoral groove to lock the extended distal limb during stance. Thus, an anatomically similar tendon-locking mechanism cannot exist in the ostrich (Gangl, 2001; Weissengruber et al., 2003)

However, structural attributes that stabilise standing posture have been previously identified in the pelvic limb of the ostrich. The acetabulum is the most centrally positioned relative to trunk length when compared to other avian species – including the other large ratites. The relatively short femur and its predominantly horizontal position during standing results in a rather small moment arm acting on the hip and knee and requires relatively little muscle force to act against over-flexion (Stolpe, 1932). Unlike most avian species, the ostrich always maintains a horizontal trunk posture that optimises stability by balancing the trunk mass naturally on top of the extended distal limbs. Additionally, the hip joint, which in all birds acts against over-flexion, is girdled in dense layers of muscle in the ostrich and is largely constrained within its 3D motion range by a strong ligamentous apparatus. This has been demonstrated in manipulation experiments after all muscles had been removed (Firbas & Zweymüller, 1972). Even with all acetabular ligaments cut, the interaction of trochanter and antitrochanter remains an osseous barrier against further over-flexion (Hertel & Campbell, 2007). Finally, the supra-jointed metatarsophalangeal posture is maintained primarily by ligaments, as observed in our present experiments with the axially loaded limb. The distinctly-oriented metatarsophalangeal joint remained elevated during all phases of loading despite the fact that all muscles and associated tendons were removed.

A striking illustration of passive limb support was seen in the course of our anatomical analyses. During reductive dissection of pelvis with limbs attached, all muscles and tendons had been removed with only skeleton and ligamentous system remaining intact. When oriented as if standing with phalangeal and distal joints extended and knee and hip flexed, the specimen had the requisite stability to stand erect when laterally balanced by hand.

Taken as a whole, it is clear that a significant amount of “work” is done by passive structures that, if absent, would require compensatory muscle power with the associated additional metabolic cost.

Prior descriptions of snap joint effects

Hildebrand (1995) identifies functioning snap joints in the ankle and elbow of certain large mammals, and describes that a ligament must cross the joint's pivot point and insert slightly beyond so that its length and tension are reduced as the joint moves in either direction from an intermediate position. He states, "Snap joints usually have at each side of the hinge either two ligaments that cross or a single broad ligament that twists. If the lateral ligament originates exactly at the pivot point then its length remains constant as the joint moves and tension does not change" and the joint cannot snap.

The avian intertarsal joint does not have a mammalian counterpart. The ostrich possesses a rather "derived" hinge joint with pronounced roll and glide qualities and coupled flexion/abduction and extension/adduction. Note also that the origins of the smaller intertarsal joint ligaments in the ostrich do, in fact, originate at the pivot point of the joint and, with the addition of condylar crests and protruding epicondyle, represent a significant variation on Hildebrand's description.

Bell (1847) and Langer (1859) both describe a "Schnappbewegung" (snapping motion) in the intertarsal joint of the ostrich and identify it as the mechanism responsible for the springy walking gait typical of many long-legged avian species. Bell (1847) posits that the LCML of the ostrich is the single constituent driving snapping motion, stating that this ligament is in a relaxed state in the depression caudal to the medial epicondyle when the intertarsal joint is extended, stretches during flexion when gliding *over* the epicondyle and returns to a relaxed state in the cranial position after passing the epicondyle. As shown in our results, this interpretation is incorrect. If the LCML were to completely traverse the epicondyle, it would be trapped in an irretrievable location. To prevent this condition, the central part of the LCML is secured from over-travel by the broad ligament originating at the medial rim of the distal tibiotarsus. Also contrary to Bell's description, the LCML remains tensed in the extended intertarsal joint to provide distal limb stability during stance phase.

Langer (1859) dismissed Bell's interpretation (1847) since he observed the springy gait in bird species (stork, flamingo, heron) that did *not* feature a prominent medial epicondyle. In the ostrich, Langer (1859) instead proposed a lateral ligament (which he does not clearly identify as the MFB) in interaction with a condylar crest as the main factor underlying the snapping effect and identifies maximum resistance at 125°.

However, Langer (1859) may have overlooked that, in wading birds, the existence of a snap mechanism without a prominent epicondyle might be explained by their much smaller size and mass in comparison to ratites. In a 5 kg stork, the arrangement of ligaments alone may be sufficient to maintain extension of the intertarsal joint to prevent over-flexion. In a 150 kg ostrich with longer effective limb length and higher CoM, more robust intertarsal joint structures (LCML/medial epicondyle and lateral ligaments/crests) are required to stabilise the distal limb to support trunk mass.

Although both Bell (1847) and Langer (1859) provide descriptions that identify components of the EDM, incomplete assessment of the isolated joint and a lack of integration of the ligaments and joint contours within a functioning whole compromise their conclusions. Neither description clearly correlates intertarsal joint behaviour with simultaneously occurring medial and lateral ligament interactions. Furthermore, they did not clarify the stabilising function of the engaged joint in *Struthio*.

To be fair, both works are quite descriptive and inclusive for their time but may have been limited by a lack of modern equipment or fresh specimens. Specimen quality may also have been the main factor in the inability of Stolpe (1932) to detect any evidence of the "snapping motion" in his examinations. Finally, none of these authors provide quantification for the inherent effects of the EDM and offer no integration of the EDM into the complete stride cycle.

Effects of the engage-disengage mechanism in the live ostrich

After qualification of the anatomical characteristics underlying the engage-disengage mechanism, we created experiments to quantify the resistance occurring when manually extending and flexing the prepared intertarsal joint. These results were subsequently applied to kinematic investigation of the intertarsal joint in walking and running ostriches to determine possible *in vivo* functions of the EDM.

The experiment with the unloaded horizontally positioned limb eliminated gravitational effects and showed that resistance from extension to flexion (9 Nm) was greater than resistance from flexion to extension (6 Nm) as illustrated in **Graph** 4.2.2.**1** in Results. This difference is primarily caused by the LCML in relation to the protruding medial epicondyle where, in full extension, it is held in position (engaged) by this protrusion and undergoes an increase in tension as it ascends the elevated epicondyle during movement towards flexion. When moving from flexion to extension, this ligament simply descends from its secured position atop the epicondyle, thus registering less resistance. These medial dynamics occur in tandem with the interplay of lateral ligaments and condylar crests. Here, when moving from extension to flexion, i.e. towards a disengaged state, the tendinous MFB encounters the distinctly elevated central crest that deflects this ligament, compounded by the resistance arising from its interaction with the LCL. The smoother, comparatively less-elevated lateral cranial crest is more easily negotiated by the MFB/LCL when transitioning towards the extended engaged state. Comparing results from the unloaded horizontal limb and the axially loaded vertical limb experiments confirmed that i) an EDM transition point of 115° was identical in both set-ups and that, ii) the highest resistance from extension to flexion occurred at 140° regardless of limb orientation or loading. This consistency indicates that these passive effects occur at identical angles in the live organism.

However, a two-fold increase in passive joint moments (18 Nm) occurred in the axially loaded limb at 140° when moving from extension to flexion compared to the unloaded limb. It is important to note the mechanical differences between the two set-ups (see **Fig.** 4.2.2.**1**, Materials & Methods). Specifically, the set-up with the unloaded limb involved rotation of the tarsometatarsus in a radial arc around the clamped tibiotarsus through the pivot point of the intertarsal joint. Since the distal end of the tarsometatarsus was the point of applied pulling force, the tarsometatarsus acted as a second-class lever against the resistance provided by the EDM at the intertarsal joint. In the second experiment, the variable of compressive loading was present through the long axis of the extended limb. In this case, the distal limb became a column with the EDM-supported intertarsal joint acting as a "spring hinge" located near the mid-point of the column.

Despite this difference in methodology, the results from these two set-ups regain relativistic significance when integrated with *in vivo* application of the intertarsal EDM in the ostrich. The unloaded limb experiment can be said to reflect the condition of the limb during swing phase – but without the effects of inertia and gravity – while the axially loaded limb experiment reflects the condition of the limb during ground contact**.** Based on these results, we hypothesise that *in vivo* intertarsal joint stability is passively augmented during all phases of ground contact since this joint never undergoes flexion below 140°. This stabilising effect could reinforce the action of intertarsal extensor muscles.

During swing phase, the unloaded joint becomes relatively free to attain flexion, or regain extension, when the phalanges are lifted off the ground. It stands to reason that inertial effects in the live ostrich limb resulting from the accelerated tarsometatarsus and toes – particularly at running speeds – might be more than sufficient to overcome any resistance towards flexion and extension when unloaded (see Results: Quantification – Resistance against extension in vertically oriented suspended limb). To test our hypothesis, we correlated the results from these experiments with kinematic data of walking and moderate-speed running ostriches.

EDM during stance phase

In both walking and intermediate speed running, the extended intertarsal joint exhibits almost no deviation from the maximally extended angle of 168° (see **Fig.** 4.2.2.**5**). In high-speed running (14.6 ms^{-1}) under maximum load the extension angle dips to a momentary low of 140° during mid-stance, corresponding with the angle of maximum resistance against flexion provided by the EDM. Thus, at any given moment of ground contact in live ostriches, the intertarsal joint never flexes beyond the minimum angle that ensures the engaged state of the EDM.

With the distal limbs of live ostriches vertically extended as in standing, the moment arm of the ground reaction force acting on the intertarsal joint is very small. This significantly reduces the flexing moment of the forces acting on this joint. Hence, moments required to neutralise this flexing action can be equally small, imparting even greater significance to the engaged state *in vivo*. In other words, although passive resistive moments against flexion are rather small at the default extended intertarsal joint angle of 168° (about 2 Nm in both the unloaded and axially loaded joint see **Graph** 4.2.2.**1**) it can be anticipated that they still contribute to a considerable extent to stabilisation of the joint.

The axially loaded ostrich limb exhibited a two-fold increase at the point of highest resistance against flexion at 140° when compared to the unloaded limb. This resulted in maximum moments of 18 Nm with a maximum vertical load application of 13.5 kg at 150° despite the corresponding reduction in columnar support arising from the now partially flexed joint. It can be hypothesised that passive extending moments may be even higher *in vivo* when considering that our experiments were performed with all tibiotarsal muscles removed and tendons running over the intertarsal joint cut through. In both intact anatomical specimens and live ostriches, the main end-tendon (*Tendo lateralis*) of the M. fibularis longus entirely overlaps the MFB after inserting at the proximal tarsometatarsus. This prominent muscle forms the cranial contour of the shank and, with origins at knee fascia, proximal fibula and the tibiotarsal Crista cnemialis, has been acknowledged as a powerful extensor of the intertarsal joint in detailed studies about ostrich limb muscle function (Gadow, 1880; Stolpe, 1932; Weissengruber et al., 2003).

In accordance with Gangl (2001), we found that the *Tendo lateralis* is firmly secured by a tendon sheath and is additionally enveloped by a strong fascia where the tendon crosses the lateral intertarsal joint space and runs directly over the MFB. Because of this stiff encasement, it was impossible to displace the *Tendo lateralis* in our intact specimens when the intertarsal joint was extended. In this state the *Tendo lateralis* presses the MFB solidly against the lateral joint surface thus constricting the MFB's ascent of the central crest. This would offer additional lateral support to the engaged joint *in vivo* and potentially increase the effectiveness of the medial epicondyle/LCML interaction by preventing luxation of the intertarsal joint. When the joint flexes in swing phase, the *Tendo lateralis* attains a relaxed state that is clearly visible in anatomical specimens by the loop it forms at the distal tibiotarsus.

The tensed M. fibularis longus is a potentially important contributor to increased passive extending moments in the intertarsal joint *in vivo*. Due to its proximity and structural connections to the MFB, the *Tendo lateralis* is functionally incorporated into the EDM when the joint is in an extended/engaged position. In this case, a ligamentous system would provide the structural basis for a tendon-locking mechanism wherein the tensed *Tendo lateralis* counters interaction of the LCML/medial epicondyle.

This interplay of joint protrusions/ligaments/reduced muscle with an intertarsal extensor end-tendon suggests that the stabilising properties of the engaged intertarsal joint may actually increase proportionally to loads encountered during stance phase. *In vivo* analyses of M. fibularis longus muscle in ground-dwelling species (*Numida meleagris* & *Meleagris gallopavo*) show a direct correlation between muscle power output and the applied load during stance phase (Ellerby & Marsh, 2006; Gabaldon et al., 2004). From this it can be deduced that tension of the *Tendo lateralis* in the ostrich increases in direct proportion to the load through the limb. This proposal will certainly require further research and should include the role of the extensors within the framework of the multi-jointed muscle-tendon complex.

A parallel beneficial characteristic of the extended distal limb appears when focusing on metatarsophalangeal joint posture during stance phase in running ostriches. Our samples show that this joint becomes increasingly flexed, i.e. is positioned closer to the ground, as speed increases (see **Fig.** 4.2.2.**5b**). The toe flexor tendons run caudally over the metatarsophalangeal joint and are proposed as the prime locus of elastic energy storage with direct load transmission ensured by the engaged intertarsal joint. This suggestion is supported by Rubenson (2007) who also observed the stiff condition of the intertarsal joint throughout stance phase in over-ground running ostriches at speeds of 3.5 ms^{-1}.

In combination with EDM-supported distal limb stiffness during ground contact, the supra-jointed metatarsophalangeal posture and its ability to sustain loading forces under flexion would provide a significant reservoir of elastic energy storage during ground contact in running and rapid release of potential energy at toe-off (e.g. Schaller et al., 2005).

EDM during swing phase

We have proposed the EDM as a positive contributor to limb stability in the engaged position. A secondary benefit of this mechanism may be seen during swing phase of the limb when the intertarsal joint enters the disengaged state shortly after toe-off, and then re-establishes an engaged position just prior to touch down.

In kinematic measurements of swing phase in walking ostriches (see **Fig.** 4.2.2.**5 a**) the intertarsal joint passes through the EDM transition point shortly after toe off resulting in a rapid and pronounced upwards trajectory of the intertarsal joint. Evidence of this effect is also present at the end of the curve in **Graph** 4.2.2.**1** at 126° where this rapid transition from an engaged to a disengaged state automatically elevates distal limb elements off the measuring scale as flexion is induced. The effect of abruptly lifting the distal limb elements vertically off the ground might prevent dragging the limb through high steppe grass when walking and presumably leads to a distinct springy gait. Just prior to touchdown, the intertarsal joint undergoes the transition from a flexed state to full extension, re-establishing the EDM-supported distal limb column in advance of loading at ground contact.

In running, there is less distinct amplitude in upward trajectory of the intertarsal joint after toe-off. However, just prior to touchdown, the intertarsal joint undergoes the EDM transition point towards extension impelling forward acceleration of the intertarsal joint. Under the conditions of the multi-jointed muscle-tendon complex, this rapid extension also extends knee, metatarsophalangeal joint and phalanges with abduction of the 4th toe, re-establishing the EDM-supported limb column in advance of loading and providing proper orientation of the ground contact elements to begin the next stride cycle.

While the proximally located limb musculature supplies force in locomotion, the passive support of the EDM, the effects of the EDM in acceleration of limb elements during swing phase and largely automated limb articulations may facilitate concentration of metabolic energy for major muscle work and neural impulse without significant diversion of energy to management of limb stabilisation and overall positioning.

Conclusions

The *bauplan* of the ostrich provides a combination of structural attributes that optimise the relationship between energy input and locomotor output. In combination with physical constraints to articulation and excursion range of the pelvic limb, we posit the EDM of the intertarsal joint as a predominantly automated system that provides both stability and impetus to the distal limb of the ostrich during all stages of locomotion. In the context of the living bird, the passive cycle of the engage-disengage mechanism and its interaction with the mandatory chain of combined joint motion reinforces strict guidance of the distal limb segments, provides automated extension of phalanges prior to touch down and substantial limb stiffness during ground contact.

The qualities of the ligamentous system in combination with skeletal features in the avian leg should be afforded greater consideration in the analysis and interpretation of terrestrial locomotion. Especially when contemplating the reconstruction of fossil taxa, functional integration of the ligaments as important contributors to bipedal locomotion would likely influence existing models that compute locomotor behaviour based largely on skeletal structure and projected muscle mass.

As a concrete example, our comparative assessment showed evidence that both extant and extinct large ratites possess similar attributes for a functionally specialised mechanism to manage high body mass during locomotion.

Considering the relationship of modern birds to their theropod ancestors, it might be interesting to imagine how we would reconstruct an ostrich if we had only the bones. Could we have known about the supra-jointed toe-posture and its advantages? Would we have inferred the auto-abduction-mechanism of the 4th toe? Could we have deduced the existence of the engage-disengage mechanism? Each of these structural attributes in the kinematic chain result in a conservation of locomotor energies. We should remain open to the idea that, in addition to the role of muscles, structures traditionally regarded as "passive" also contribute to locomotor efficiency and can provide significant biomechanical advantages without the consumption of additional metabolic energy.

Future investigations will incorporate a more diverse sample group including juvenile to 15 year-old ostriches. Variables in our calculations, including bone segment lengths, will change according to specimen age in tandem with increasing ligament calcification, requiring comparative analyses of ligament fibre properties. In addition, the related large ratites should be part of an inter-specific comparison employing identical methodologies to establish species-specific characteristics of the EDM.

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4.2.3 Dynamic analysis of phalangeal load and pressure distribution

The ostrich (*Struthio camelus*), emu and rhea (ratites) inhabit desert and steppe-like environments and rely on their speed and endurance to outrun predators and cover vast distances. Ratite locomotion receives increasing interest from various disciplines as these flightless cursorial bird species are considered a valuable model for the reconstruction of possible locomotor modes among theropod dinosaurs, the ancestors of modern birds (Farlow et al., 2000; Gatesy, 1991). In contrast to many other birds, ostriches are unable to grasp since the degree of toe flexion is very limited due to its phalangeal anatomy. The range of leg motion is essentially limited to the fore/aft plane, including instances of forward kicking as a mode of defence. Thus, *Struthio camelus* provides a particularly good example of adaptation toward uni-functional limbs, as would be expected of an animal capable of extreme speed and exceptional endurance.

The highly cursorial lifestyle of these birds has inspired a number of kinematic and kinetic studies (e.g. Abourachid & Renous, 2000; Gatesy & Biewener, 1991), including examination of metabolic rates during treadmill exercise and 3D analysis of articular motion range in over-ground running (e.g. Rubenson et al., 2004, 2007). While existing inquiries generally focussed on over-all body posture and particularly on hind limb kinematics, there has been no exploration of the dynamics of toes as ground contact elements during the time between touch-down and toe-off. Although technological advances within the last decade have enabled detailed studies of terrestrial locomotion in birds including turkey, guinea fowl, magpie and ratites, options for examination of toe function were limited to measurements using force plates without integration of pressure data. The only surveys regarding phalangeal function are ichnotaxonomic analyses comparing modern ostrich and emu with preserved theropod track-ways in order to reconstruct theropod gait patterns (Farlow, 1989; Milan, 2006; Padian & Olsen, 1989). Although this is a feasible approach within the paleontological aim, these techniques deliver a static depth profile and provide no direct information regarding temporal parameters of load distribution throughout ground contact.

As the link between and animal and substrate, the dynamics of phalangeal interaction with the substrate allows detailed interpretation of toe function. This critical relationship is magnified at running velocities when ground contact duration (GCD) is relatively short and only one 'foot' at a time makes ground contact. At touch-down, movement of the phalanges is abruptly arrested and forces exerted by the body mass must be managed. As the body travels over the area of phalangeal support, the toes must be firmly 'installed' on the substrate and, at toe-off, provide energetic propulsion for the continuation of the stride cycle. This examination of the interplay of toes and their functional relationship to the substrate expands the understanding of locomotor performance in cursorial bird species and complements existing knowledge about gross kinematics.

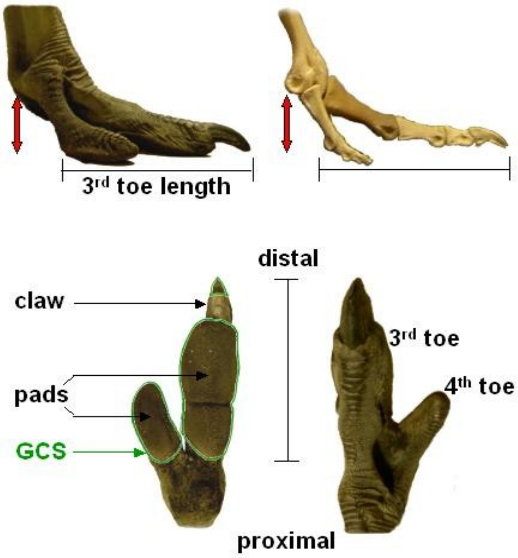

Fig. 4.2.3.**1:** Right phalanges of adult ostrich.

Towards this end, we examined toe function in the ostrich which is able to run steadily for 30 minutes with an average speed of 60 kmh^{-1} (Alexander et al., 1979; Grzimek & Grzimek, 1959; Hallam, 1991). This unmatched running performance establishes the ostrich as the fastest extant long-endurance biped, providing a valuable model for our inquiry.

Struthio exhibits distinct specialisations of ground contact elements related to its cursorial lifestyle (**Fig.** 4.2.3.**1**). While most bird species have four digits – generally three pointing forwards and one pointing backwards (anisodactyle) or two pointing forwards and two pointing backwards (zygo- and heterodactyle) – emu and rhea decreased their toe number to three by eliminating the posterior digit V (tridactyle). The ostrich further reduced the innermost digit II leaving only the 3rd major claw-bearing toe and the 4th minor toe, establishing the ostrich as the only extant didactyle bird (digits III & IV). It is generally appreciated that this toe reduction reflects a progressive step towards locomotor performance in the ostrich, resulting in a highly concentrated traction surface when compared to the three-toed ratites and is further comparable to the evolution of horses with reduction from five toes to one (Gangl, 2001; Hallam, 1992; Weissengruber et al., 2003). This toe reduction partially eliminates the need for corresponding musculature thus decreasing mass at the distal end of the swinging leg in addition to the characteristic ratite elongation of distal hind limb elements (e.g. Schaller et al., 2005). Persistent scientific debate proposing further reduction and eventual elimination of the 4th toe arises from the perspective that evolutionary imperatives dictate a gradual, but ceaseless, discarding of structures and functions that are deemed biologically redundant. Although the reduction from three toes to two in the ostrich certainly appears to reflect an evolutionary progression, possible 4th toe reduction must be considered within the context of the ostrich as a biped – along with the consequences to Base of Support (BoS) – as opposed to the typical example of phalangeal reduction in the quadrupedal horse (e.g. Hof, 2008; Kummer, 1956).

Our previous anatomical examination showed that the plantar surfaces of the toes are similar to those of the camel with a leathery appearance and durable sole covered in dense papillae, suitable for locomotion on various substrates. The phalangeal skeleton of both toes is enveloped in a pair of fat-pads to protect the bones, absorb high transient stresses and conform to the substrate. Generally, it can be said that the toes of the ostrich are unlike those of most other avian species with only the other large ratites possessing similar ground contact elements. The intersection between the two pads on 3rd and 4th toe in the ostrich does not correspond to the location of an interphalangeal joint as seen in the emu (Milan, 2006) and the ostrich is the only bird featuring just a single claw prominently situated at the 3rd toe tip (**Fig.** 4.2.3.**1**).

Another unique adaptation of the ground contact surface is seen in the permanent elevation of the proximal phalanx of both toes above the ground plane (Deeming, 1999; Kistner & Reiner, 2002), resulting in what we refer to as the supra-jointed toe-posture. The functional de-coupling of this phalanx from the actual 'foot' achieves an additional decrease in traction surface. Moreover, studies suggest that the elevated metatarsophalangeal joint of the ostrich also serves as a shock absorber and contributes to elastic energy storage and reflection capacities – an important factor in fast and steady locomotion (Rubenson et al., 2007; Schaller et al., 2005). These varied strategies and specialisations, including toe reduction, mass reduction/redistribution, reduction of traction surface and dynamic energy storage capacities presumably combine to allow higher stride frequency at lower metabolic cost, a precondition for the coexistence of speed and endurance.

In order to examine dynamics of the 3rd and 4th toe *in vivo*, we employed pedobarography as our primary data acquisition method. This technique is routinely used in the orthopaedic and sports sciences and has recently been established as a reliable methodology in the study of locomotor dynamics in various mammalian species (e.g. D'Août et al., 2004; De Cock et al., 2005; Hallemans et al., 2003; Van der Tot et al., 2002, 2003, 2004, 2005; Vereecke et al., 2003, 2005).

Samples obtained using the pressure plate allow us to:

1. capture spatio-temporal pressure distribution for the entire ground contact surface (GCS) at high resolution to determine relative phalangeal loading throughout ground contact
2. track the Centre of Pressure (CoP) trajectory within phalangeal ground contact elements
3. observe relative toe position, infer functional relationship and analyse adjustments to 4th toe position and load at various locomotor speeds
4. integrate observations of manual extension of knee leading to 4th toe abduction in anatomical specimens with *in vivo* data. Since this effect persisted once all muscles/tendons were removed, we will investigate whether this abduction could be part of an automated mechanism.

Materials and methods

Pedobarographic measurements

The ostriches used in this study are kept year-round in an outdoor enclosure of grassland (6400 m²) near Heidelberg, Germany (**Fig.** 4.2.3.**2**). The birds have *ad lib.* access to water, pasturage and ostrich fodder with seasonally-dependant composition. Living conditions are in accordance with the official guidelines for ostrich-keeping as regulated by German law. The birds have not been subjected to surgery or any form of invasive physical manipulation. The ostrich chicks were purchased from a local breeder in 2004 and hand-raised from the age of ten weeks to foster acceptance of human contact and become familiar with the experimental corridor that was also used in parallel kinematic studies. The near-daily presence of the experimenter over a period of years allowed these experiments to yield a large number of high quality samples in a relatively short three-day time frame.

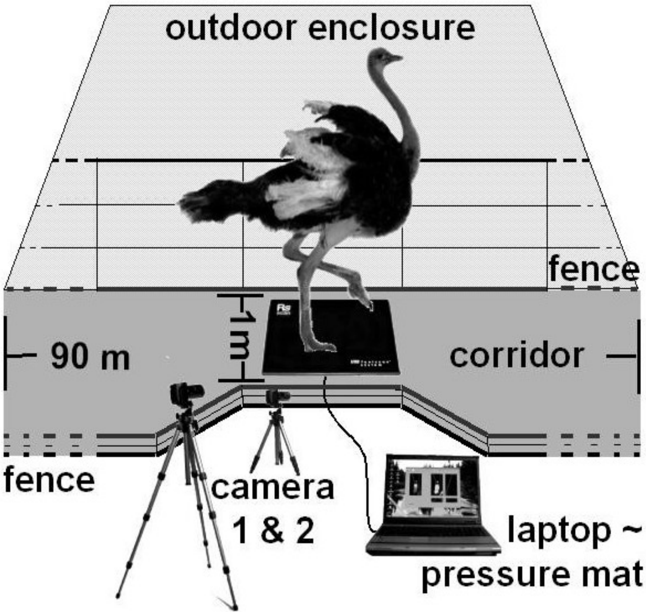

Fig. 4.2.3.**2**: On-site data acquisition system

A total of five ostriches were previously recorded (Schaller et al., 2006), but this study focuses on two specimens. Experiments were carried out with full-grown co-operative female ostriches (*Struthio camelus australis*; 3-year-old/ca. 90 kg) during September 2006 (3 recording days) under stable weather conditions (sunny, slight overcast, ~ 20 °C).

A 90 m long x 3 m wide corridor was separated from the main enclosure by wire mesh and narrowed to 1 m wide where the data acquisition system was located (**Fig.** 4.2.3.**2**). The set-up consisted of one RSscan International® pressure plate (45 x 30 cm, 250-Hz sampling & 16,384 pressure sensors of 0.375 cm^2, USBII interface) measuring dynamic phalangeal pressure distribution. The plate was contained in a specifically designed frame to stabilise position and was covered with a thin non-slip rubber sheet to prevent damage caused by the 3rd toe claw. To ensure perfectly level orientation, the pressure plate/frame was placed within damp sand and level conditions were confirmed at 10 min. intervals using a water-level. Data acquisition and subsequent data processing were carried out using Footscan MST software 6.2 & 6.3 (RSscan International®). One digital camera (Canon MV 900; 50 fps) recorded overall body posture and a second camera (Canon MV 550i; 50 fps) synchronised with camera 1, recorded detail of the phalanges during ground contact. Cameras were perpendicular to the sagittal plane of motion.

We obtained samples of slow walking to moderate running gaits (0.3 – 6 ms^{-1}). Ostriches performed without physical manipulation and chose their favoured velocities, ensuring that data reflected a natural stride cycle. When not spontaneous, locomotion was initiated either by display of food at the end of the corridor or by the ostrich-keeper walking/running ahead to compel the ostrich to follow. A total of 200 samples were yielded and subsequently assessed to determine the distribution of ground contact duration relative to speed. For phalangeal pressure distribution and CoP analysis, 114 samples were deemed usable with partial footfalls and unsteady manoeuvres omitted. The CoP trajectory was calculated as a function of time. Changes to CoP trajectory at various speeds were tracked by creating a set of graphical representations of samples with GCD increments of 10 frames (0.4 sec.).

The pressure plate was used outside of its typical application and thus pressure values are given in arbitrary units (a.u.) as opposed to an absolute magnitude. Since the primary aim is to establish the relative participation of phalangeal elements during ground contact, absolute load values are of lesser interest in this study. Regardless, it is estimated that 1 a.u. is equal to 1 N (± 10%).

A series of measurements were derived from the toe pressure profiles including: 1) functional 3rd toe length, i.e. the distance between the most proximal part of the ground contact zone (second phalanx) and the tip of the 3rd toe claw, 2) degree of abduction, i.e. angle between the longitudinal axis of 3rd and 4th toe, and 3) ground contact duration (**Fig.** 4.2.3.**3**). Velocity (v) was estimated on the basis of the lateral full-body video images relative to visual markers installed at 1 m increments on the corridor fence. All complete footfall samples were synchronised with their corresponding video sequences inclusive of full body and close-up views. Samples referred to as "running" were classified based on velocity (v > 3 ms^{-1}) and not by duty factor since it has been reported that ostriches employ a bouncy running gait with a duty factor > 0.5 (Rubenson, 2004). It should be noted that this paper does not intend to define a boundary between walking and running but rather seeks to determine, on a comparative basis, how differences in velocity and gait affect CoP.

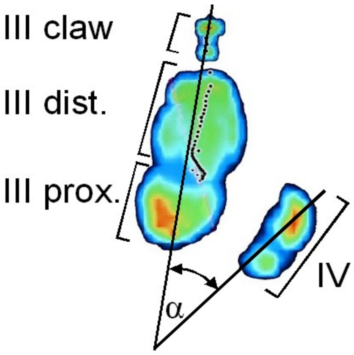

Fig. 4.2.3.**3**: Footscan image of a running sequence. Loads are indicated on a gradient from red (very high) to dark blue (very low). Partially dotted line illustrates CoP path (dot interspace: 4 msec.). α = angle between main axis of 3rd & 4th toe.

On the basis of external morphology, we established three major toe regions: 1) the 3rd toe, 2) the claw-tip of the 3rd toe and 3) the 4th toe. For each toe region, the average pressure was plotted as a function of time, which was normalised against the total ground contact duration of all elements. Additionally, we assessed four areas of highest load distribution over time for 1) the claw-tip (III cl.), 2) the 4th toe (IV), 3) the proximal (III pr.) and 4) the distal end of the 3rd toe (III di.; **Fig.** 4.2.3.**3**). Each area is defined by a square of 2 x 2 sensors (10.16 by 15.24 mm^2). Statistical analyses were calculated using ANOVA[b].

Manual manipulation and macroscopic dissections of two lower ostrich limbs

Prior to slaughter, a live ostrich (14 months, 105 kg) comparable in size and dimensions to our specimens was assessed within its enclosure to ensure a properly elevated metatarsophalangeal joint and normal, healthy locomotor patterns without articular dysfunction. This freshly slaughtered ostrich was subjected to on-site manipulation to explore automated phalangeal articulation with emphasis on the 4th toe ab-/adduction mechanism. 4th toe abduction was induced by knee extension and adduction by knee flexion respectively. Additionally, toe prints were collected for reference as described below. Subsequently, sub-intertarsal joint preparations were manipulated under laboratory conditions to determine possible changes in the automated 4th toe ab-/adduction after tendons were severed. All stages of manual manipulation were video recorded in frontal and lateral views (distance to object 1 m, camera 1 and 2 positioned at a 90°) using the camera equipment described above. Finally, the fresh sub-intertarsal joint preparations were macroscopically dissected in order to determine the anatomical basis for the automated 4th toe ab-/ adduction.

Orthopaedic foam track capture of ostriches

Orthopaedic foam was used to collect toe prints of anatomical specimens and live ostriches. When exposed to the pressure exerted by a footfall, this industry-standard pressure-sensitive foam retains the exact shape of the distorting element to preserve a highly detailed impression. Toe prints of live ostriches were sampled with our own birds in the outdoor enclosure near Heidelberg (Germany). Additional experiments explored variation in toe positioning among our live and fresh anatomical specimens with focus on the 4th toe abduction automatism. Both the entire hind limbs and distal limb elements of recently slaughtered ostriches were used to determine toe articulation range and the extent to which passive structures in the limb affect this motion range. Toe prints were obtained by exerting pressure on the proximal part of the limb in a downward vertical direction to create an impression of the toes in the orthopaedic foam with i) the knee and intertarsal joint extended and ii) the tarsometatarsus in a vertical position and the 3rd toe maximally extended. In each of the described limb and toe postures, we observed the automatic abduction of the 4th toe characteristic of live birds prior to touch down. The foam imprints allowed us to analyse the degree of automated 4th toe abduction and over-all motility of the minor toe. These toe prints also served as a control group to compare area of phalangeal surfaces with the data yielded by the pressure plate recordings.

Results

The relationship between Ground Contact Duration (GCD) and velocity was determined by combining pressure plate data with video footage. Velocities between 3 to 6 ms^{-1} were classified as running gaits. A conventional definition for running derived from duty factor (DF) < 0.5 was not applied since ostriches also employ grounded running gaits with DF > 0.5 (Rubenson, 2004).

Speeds between 1.6 to 3 ms^{-1} occupy a transition zone in which the birds either accelerated or decelerated. Walking speeds were defined at 1.0 to 1.6 ms^{-1} where the ostriches moved in a steady forward direction. When velocities fell below ~ 1.0 ms^{-1}, unsteady gaits became the norm and incorporation of these samples did not reflect the intent of this study. Particularly at GCD exceeding 1.7 sec., as seen in grazing, we observed asynchronous swing phases in the legs with unequal step lengths over two stride cycles or ground contact duration that varied for left and right phalanges within one stride. Hence, these samples were disregarded in the context of walking but are included in **Table Fig.** 4.2.3.**1** and **Fig.** 4.2.3.**4** for completeness as grey bars to the right of the dashed line.

Table 4.2.3.**1:** Relationship between velocity and GCD

	RUNNING			TRANSITION	WALKING	Unsteady W.	GRAZING	
frames	< 90	90 - 120	121 - 140	141 - 280	280 - 400	401 - 500	501 - 700	701 - 999
GCD (sec)	0.3	0.32 – 0.40	0.40 – 0.47	0.47 – 0.93	0.93 – 1.3	1.3 – 1.7	1.7 – 2.3	2.3 – 3.0
υ (ms^{-1})	6.0	5.0 – 4.0	4.0 – 3.0	3.0 – 1.5	1.6 – 1.0	1.0 – 0.8	0.8– 0.7	0.7 – 0.3

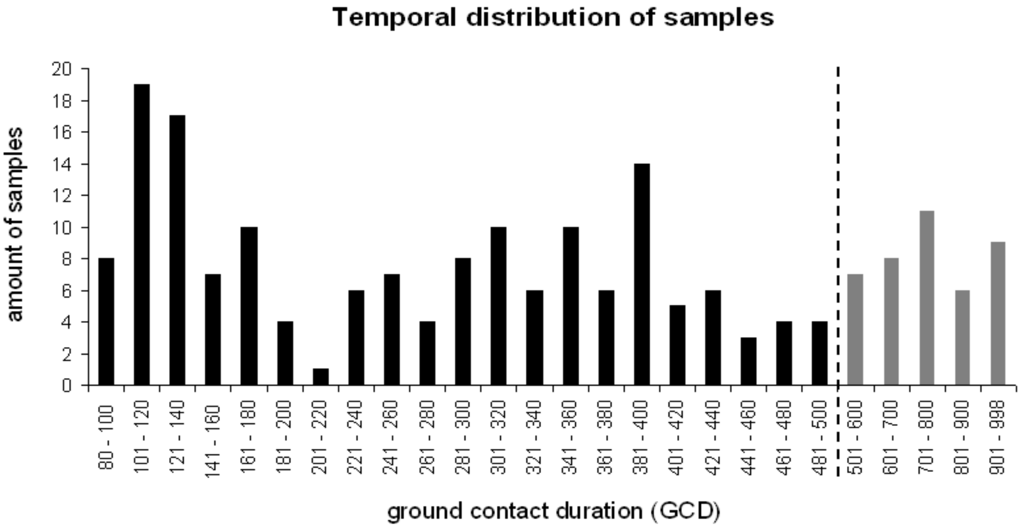

Fig. 4.2.3.**4:** Temporal distribution of samples where 300 frames of GCD equal 1 sec.
Distribution from frames 500 to 998 appear in increments of 100 due to low sample number.

The temporal distribution of the total number of ground contact samples is quite concentrated in the GCD range of 0.3 – 0.47 sec. From GCD 0.47 – 0.93 very few samples were obtained. This may be explained by the fact that, as mentioned above, this range of GCD reflects an intermediate locomotor phase of acceleration-deceleration representing the transition between running and walking speeds.

Phalangeal load distribution

Table 4.2.3.**2** shows the averaged value of total ground contact surface area (TGCS) and segmental ground contact surface area (SGCS) for right and left phalanges in the specimens used in this study:

Table 4.2.3.**2**: 3rd toe length and ground contact surface areas of phalanges

3rd toe length incl. claw tip (n = 2)	19.6 cm ± 1 cm
TGCS (n = 2)	80.7 cm² ± 1 cm²
SGCS 3rd toe surface area	57.5 cm² ± 0.5 cm²
SGCS claw	4.1 cm² ± 0.25 cm²
SGCS 4th toe	19.1 cm² ± 0.25 cm²

Walking

The following ground contact data represents walking speeds and was typical starting at GCD of 0.93 sec and remained persistent to a GCD of 1.5 sec. The integrated pressure curve for all three ground contact elements (3rd toe, claw, 4th toe) in walking is shown on the left in **Fig.** 4.2.3.**5**. Peak integrated pressure occurred at 70% of ground contact duration with a value of 1660 arbitrary units (a.u.) and a standard deviation of 34%. The 4th toe was the first element to reach maximum load in the time-bracket from 20% to 45% of GCD with a peak pressure of 235 a.u. and a substantial standard deviation of 70%. The 3rd toe was subjected to maximum load from 60% to 75% of GCD with a peak pressure of 1530 a.u. and a standard deviation of 37%. Since 3rd toe peak pressure was 93% of total phalangeal load-bearing, it largely influenced the timing of integrated peak pressure. The 3rd toe claw achieved only negligible ground contact through the majority of GCD, averaging only 1.63% of integrated pressure value with a short peak at push-off due to its overhanging length beyond the 3rd toe tip. With the exception of incidental contact at toe-off, the claw is essentially uninvolved in locomotion during stable level-ground walking on a predictable substrate.

At touch-down, load generally increased simultaneously at the proximal and distal portion of the 3rd toe (**Fig.** 4.2.3.**6, a-d**) until the last third of GCD when load shifted to the distal area of the 3rd toe reaching its maximum value shortly before push-off. While 3rd toe pressure values followed a common LD pattern, the participation of the significantly smaller 4th toe appeared relatively unpredictable with a nominal value of 19.5% of load at peak pressure. As indicated by the high standard deviation, the 4th toe registered loads up to 70% above and below this value. Samples at the extreme margins of the group indicated that the 4th toe bore a low of 3% and a high of 50% of the entire load during the initial phase of ground contact. Due to the didactyle “foot” of the ostrich, and with walking loads consequently shared by 3rd and 4th toe, high load-bearing in the 4th toe resulted in relatively lower load-bearing in the 3rd toe (**Fig.** 4.2.3.**5**).

Fig. 4.2.3.**5**: Load distribution in walking and running

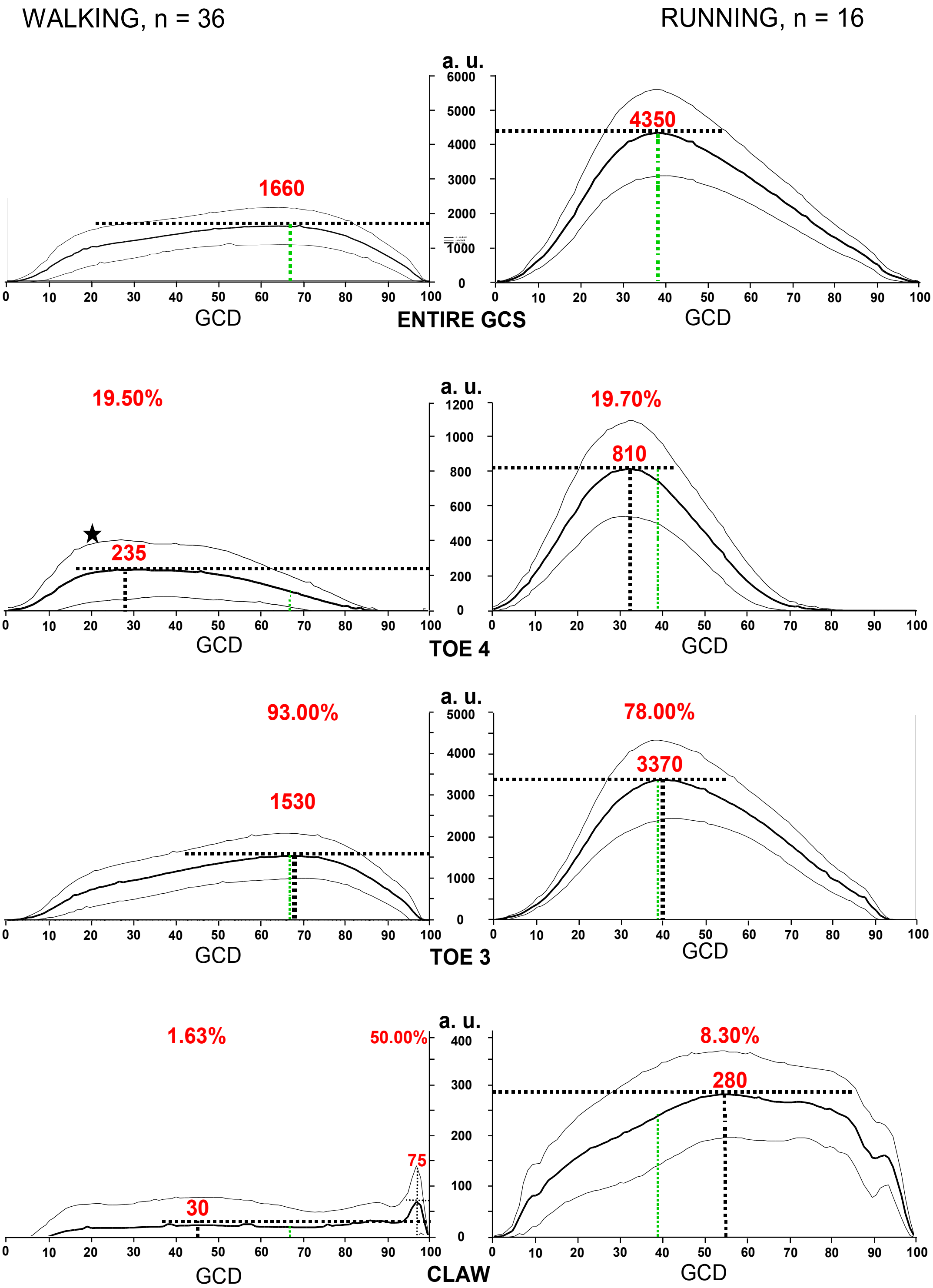

Fig. 4.2.3.**6**: LD and CoP-PATH

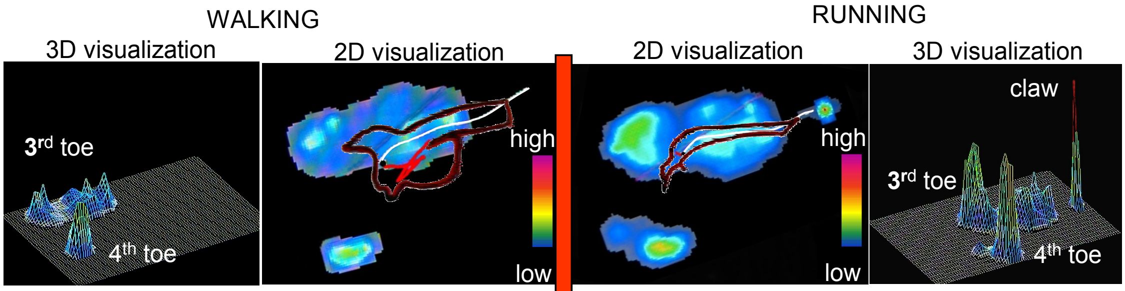

Fig. 6a: Touch-down phase, sample 54/361 (15% GCD); red = completed CoP-Path. Dark red contour indicates CoP distribution.

Fig. 6e: Touch-down phase, sample 16/102 (15% GCD); white = remaining CoP path. Dark red contour indicates CoP distribution.

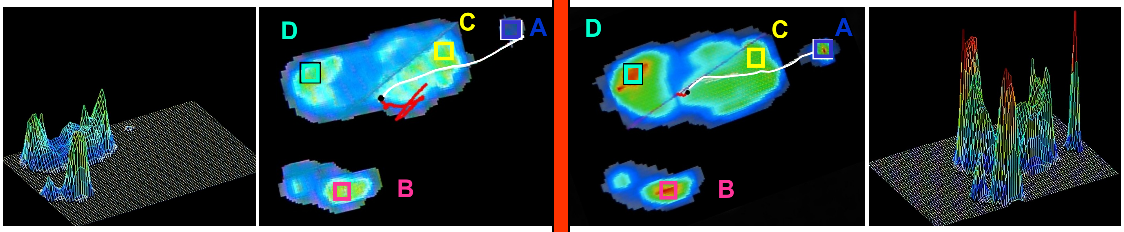

Fig. 6b: Midstance phase, sample 180/361 (50% GCD); Four sensors located at points of highest pressure for claw (A), 4th toe (B) and 3rd toe (C & D)

Fig. 6f: Midstance phase, sample 51/102 (50% GCD); Four sensors located at points of highest pressure for claw (A), 4th toe (B) and 3rd toe (C & D)

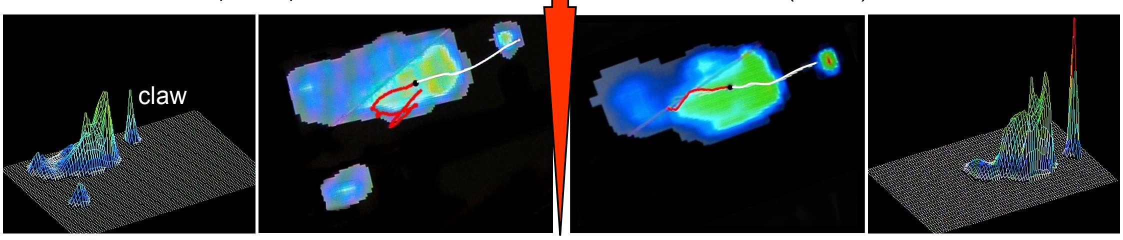

Fig. 6c: Early push-off phase, sample 308/361 (85% GCD)

Fig. 6g: Early push-off phase, sample 86/102 (85% GCD)

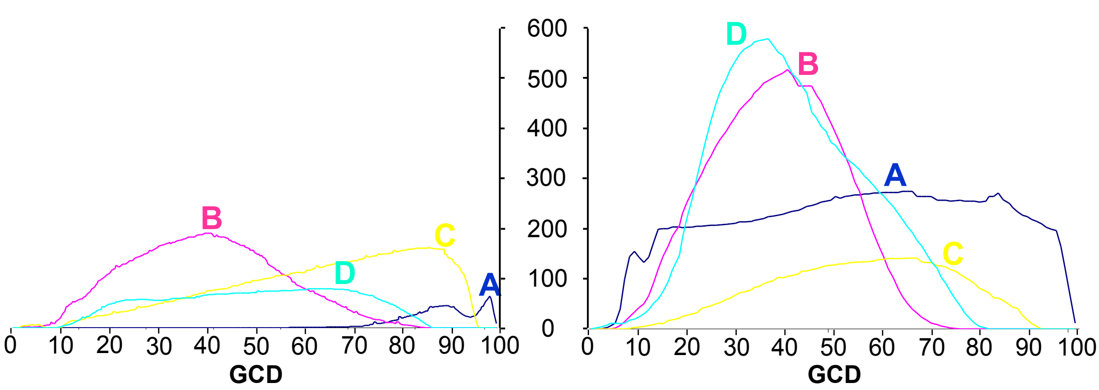

Fig. 6d: Discrete pressure data for four sensor points through GCD (corresponding to Fig. 3b)

Fig. 6h: Discrete pressure data for four sensor points through GCD (corresponding to Fig. 4b)

Moderate-speed running

The following ground contact data was typical of running speeds starting at GCD of 0.3 sec. through to GCD of 0.47 sec. The integrated pressure curve for all three ground contact elements in running is shown on the right in **Fig.** 4.2.3.**5**. Peak integrated pressure occurred at 37% of ground contact duration with a value of 4350 a.u. and a standard deviation of 28%. The 4th toe was the first element to reach momentary maximum load at 32% of GCD with a peak pressure of 810 a.u. and a standard deviation of 35%. The 3rd toe maximum load occurred at 40% of GCD with a peak pressure of 3370 a.u. and a standard deviation of 26%. As in walking trials, 3rd toe peak pressure was substantial at 78% of total phalangeal load bearing through GCD, and also largely influenced the timing of peak integrated pressure but occurred much closer to the peak time of the 4th toe.

In contrast to the near-absent values in walking, the 3rd toe claw played a much more active role in running with maximum load values at 55% of GCD with a peak pressure of 280 a.u. and a standard deviation of 29%, with a second smaller peak occurring just prior to toe-off once the claw was the only remaining ground contact element, with a final increase of pressure exerted at push-off.

The load distribution curve in running samples showed a predictably different contour from the curve seen in walking with a rather sharp peak at 40% of GCD and very short peak times for 3rd and 4th toes and a longer, more evenly distributed pressure curve for the claw. Due to the shorter GCD in running, near-simultaneous application of high load was seen on the proximal segment of the 3rd toe (78% of total load at peak pressure), tip of the 4th toe (19.7% of total load at peak pressure) and claw (8.3% of total load at peak pressure). This pressure distribution pattern reflects the tripod-like arrangement of ground contact elements evident throughout the running samples (**Fig.** 4.2.3.**6, e-g**). In contrast to walking, the claw sustained load throughout the entire GCD with video footage confirming that the claw struck the plate concurrently with other elements and remained planted during the entire GCD (**Fig.** 4.2.3.**6, h**). As the speed of the ostriches decreased, the integrated pressure peak seen in the initial 33% of GCD flattened and shifted towards the 70% point of GCD as walking speeds were approached (**Fig.** 4.2.3.**5**).

Key comparisons between walking and running

As expected, absolute load values were substantially higher in running due to the effects of increased inertial body mass resulting in higher ground reaction forces (GRF). In both walking and running, the 4th toe reached peak pressure values first, followed by 3rd toe and finally the claw. However, the maxima in running occurred within a much smaller time frame in both absolute and relative terms where maximum load bearing of 3rd and 4th toe in the first third of GCD is reflected in the peak for the entire ground contact surface. In walking, only the 4th toe attained its maximum load in the first third of GCD. The high standard deviation in the 4th toe (**Fig.** 4.2.3.**5**, 4th toe curve, see star) and the resulting intermittent values up to 50% of total load in the initial stage of ground contact is quite significant considering a 1:3 surface area ratio of 4th toe to 3rd toe. In walking, the 3rd toe generally supported the majority of load but participated to a lesser degree in samples with high initial 4th toe load values.

A substantial difference in phalangeal expression during ground contact is evident when comparing walking and running samples. In walking, the temporal sequence of ground contact among elements resembles the "roll-on/roll-off" characteristic of a human footfall. The sequence essentially starts with a "heel strike" provided by the proximal part of 3rd toe combined with 4th toe, transitions through a slightly arched central portion of the "foot" and proceeds to maximum integrated pressure value shortly before toe-off, largely supported by the distal portion of the 3rd toe. The long, relatively flat integrated pressure curve reflects the gradual phasing of load forces over the GCD.

In running samples the sharp, relatively peaked integrated pressure curve reflects the sudden rise of load forces present at the beginning of ground contact with peak value reached prior to 50% of GCD. Longitudinal mid-point segmentation of the 3rd toe forms a dual-purpose arch during running (see **Fig.** 4.2.3.**6, f**) and results in distribution of load between the proximal 3rd toe and distal claw with generally negligible loads measured at the distal 3rd and proximal 4th toe areas. This arch establishes load distribution in the tripod pattern and ensures that the claw tip is oriented downward to penetrate the ground and guarantee solid contact with the substrate.

The smoother persistent LD curve of the claw establishes the important role of this element as a positional anchor during ground contact. In the last 10% of GCD, the claw is the only grounded element but the CoM of the ostrich is now far ahead of this point of contact and overall load bearing is low.

Inter- and intra-individual variation of LD in walking and running

Standard deviations (SD) for LD data appear high in both walking and running, particularly in the range of peak values, and are more pronounced throughout GCD in the 4th toe. However, in the fastest trials, the SD of both Integrated Pressure and the four areas of highest pressure within the GCS were less than seen in walking. This is to be expected as higher velocities result in greater dynamic stability, reflected in more consistent toe positioning and greater synchrony in phalangeal inter-relationship at touch-down. Statistical analysis showed that there was no significant inter-individual variation in either walking or running trials.

CoP path in walking and running

In walking, the CoP path traversed a larger area and was generally less consistent than in running. This can be attributed to the spatial distribution of CoP origin at the initial phase of ground contact in walking (**Fig.** 4.2.3.**6, a**) where, in the initial 15% of GCD, the CoP appeared within a significantly larger area than seen in running samples (**Fig.** 4.2.3.**6, e**). At 70% of GCD, CoP was located close to the lateral edge/middle of the 3rd toe, and finally travelled rectilinearly/distally, resolving with a rapid push through the claw-tip (Fig. 4.2.3.**6, b-c**). Generally, CoP never originated medially of the longitudinal axis of the 3rd toe. There was close correlation between decreased speed and increased divergence of CoP path see **Fig.** 4.2.3.**6 a**.

As opposed to walking gaits, CoP origin during running consistently fell within a defined area located at, or just lateral to, the arch of the 3rd toe (**Fig.** 4.2.3.**6, e**). Within the first 15% of GCD, CoP migrated to the longitudinal centre of the 3rd toe where it remained for ~ 70% of GCD thereafter continuing in an anterograde direction and finally resolving at the tip of the claw at push-off.

Dextrality in ostriches

When grouping Footscan samples based on GCD and dividing samples from left and right phalanges we saw that, while the shape of the CoP trajectory itself was similar, it was regularly shifted more laterally in the left toe-print of Specimen 1 regardless of the direction from which the ostrich approached the pressure plate. This suggests that ostriches – like human beings – may exhibit some degree of dextrality resulting in asymmetrical angles of approach to touch down. This was seen in samples where the 4th toe showed high load-bearing values and clearly influenced CoP origin.

Position of the 4th toe at walking and running speeds

Pressure plate recordings and subsequent graphical overlapping showed slight variations in 4th toe position that appeared independent of gait type and GCD. However, as speed decreased, positional variation in 4th toe increased. This finding was somewhat unexpected since our previous manipulation experiments with fresh anatomical specimens revealed that manual extension of the knee joint in an isolated hind limb of a dead ostrich (before/after *Rigor mortis*) caused simultaneous intertarsal and metatarsophalangeal joint extension coupled with automatic 4th toe abduction to a default angle of 28° relative to the long axis of the 3rd toe. We then tested whether automated 4th toe abduction could also be induced by manually extending the 3rd toe. This again led to self-directed 4th toe abduction to a 28° angle relative to 3rd toe. Conversely, flexing the 3rd toe caused the 4th toe to automatically adduct and, at maximum flexion of the metatarsophalangeal joint, was partially overlapped by the major toe. This automation persisted in the isolated tarsometatarsal/phalangeal complex after removal of the tibiotarsus, including severance of all toe-actuating tendons of the pelvic, thigh and tibiotarsal muscles. With the 3rd toe held in a fixed position, the maximum motion range of the 4th toe during ab- and adduction was 11 cm in the up/down direction (**Fig.** 4.2.3.**7**). The mediolateral motion range amounted to 4.5 cm, resulting in a maximum angle of 34° between main axis of 3rd and 4th toe. The maximum cranial/caudal motion range was 2 cm, resulting in angles from 22° to 34° relative to 3rd toe.

Illustration of 4th toe motion range is presented in imprints made with orthopaedic foam capturing maximal motion range displacement. Imprints were created in which the 4th toe was 1) maximally abducted, 2) maximally adducted, 3) positioned most proximally and 4) most distally (**Fig.** 4.2.3.**8**).

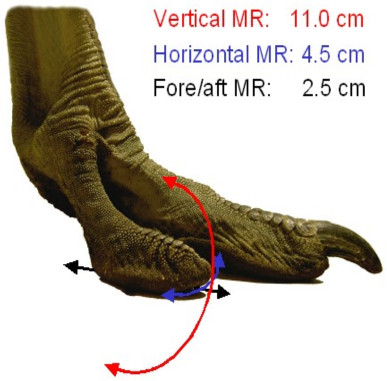

Fig. 4.2.3.**7**: Motion range of 4th toe.

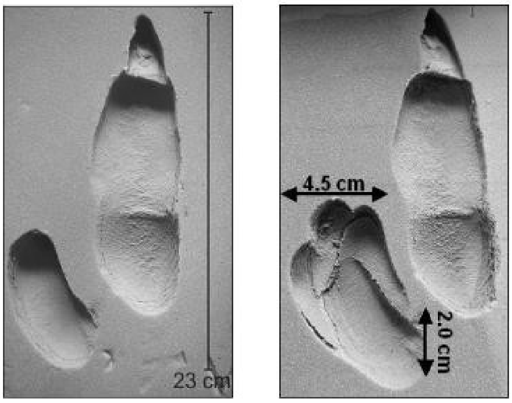

Fig. 4.2.3.**8**: Left image shows imprint of default toe position, right side depicts maximum motion range of 4th toe medially and laterally of default imprint.

Qualification of passive elements involved in 4th toe automatism and identification of muscles allowing fine adjustment

With skin and fat pads completely removed, the 3rd toe was once again flexed and extended. The 4th toe still exhibited automatic ad- and abduction. Dissection revealed that one prominent interphalangeal ligament ensured this effect due to its orientation and points of insertion between the 3rd and 4th phalanges, limiting abduction over 34° (**Fig.** 4.2.3.**9**). After cutting the ligament, the automated positioning effect was entirely absent. This interphalangeal ligament originates lateroproximally at the Phalanx proximalis of the 3rd toe and inserts medioproximally at the second Phalanx intermedialis of the 4th toe. In the course of abduction through manual 3rd toe extension, we saw that the 4th toe was not only abducted but also rotated slightly outwards. This slight rotation of the 4th toe and the diagonal orientation of the ligament kept the latter taut at all times and automatically regulated the degree of ab- or adduction depending on the degree of 3rd toe flexion/extension.

Due to observed areas of origin and insertion, we suggest that the following muscles are responsible for fine-tuning the 4th toe: M. abductor digiti IV with insertion laterally at the first phalanx of 4th toe, M. flexor perforatus digiti IV with insertion at the 4th toe at the phalanx ungualis and at 3rd toe at Tuberculum flexorium of Phalanx ungualis III and M. flexor hallucis longus.

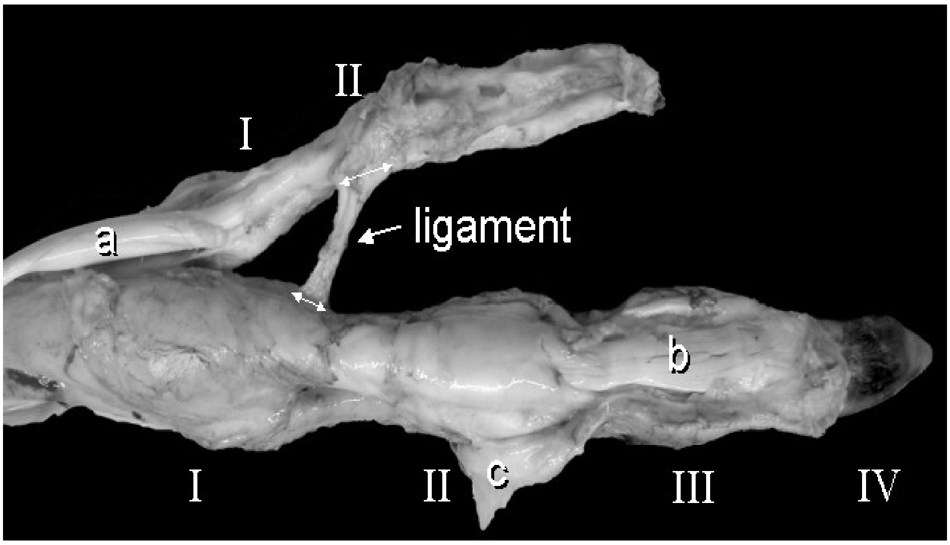

Fig. 4.2.3.**9**: Right phalanges of adult ostrich, plantar view.
Roman numbers indicate specific phalanx, a = tendon of M. flexor perforatus digiti IV, b = tendon of M.flexor perforans et perforatus digiti III, c = enhanced fascia.

Discussion

Pedobarographic methodology allows detailed functional analysis of ground contact elements

This study presents first-time pedobarographic analysis of phalangeal pressure and load distribution in the ostrich which, as a flightless bird, is limited exclusively to terrestrial locomotion. Merging the large number of samples obtained in our experiments with the apparent consistency of LD and CoP path found in walking and running samples forms a reliable data-base for the interpretation of toe function in *Struthio*.

The position and orientation of the 3rd toe and its prominent claw – essentially forming an elongation of the tarsometatarsal main limb axis – ensures reliable load-bearing and stable grip at running speeds. This functional elongation of the limb is enveloped by a very rigid nexus of ligaments, fascia and shock-absorbing fat-pads around the phalanges and interphalangeal joints of the 3rd toe. Together, these structures constrain mobility of the phalanges within a very limited range of internal flexion/extension during ground contact and eliminate mediolateral movement. This anatomical condition can be reasonably compared to the functionally conjoined hoof and tarsus in the horse and establishes the 3rd toe as the main load-bearing element in all phases of locomotion.

As a consequence of its limited range of motion, the 3rd toe is unable to contribute active compensation for the maintenance of balance in the lateral plane and is employed as the main structural interface with the ground surface to provide significant load bearing, shock absorption and grip on the substrate *via* the claw.

The 4th toe is the only ground contact element that can achieve a degree of "voluntary" fine adjustment due to its inherently greater three-dimensional motion range. Evidence of this function is apparent in the relatively high standard deviation values in load distribution, especially compared to 3rd toe. Instead of indicating variability in nominal pressure values resulting from individual differences in morphology, standard deviation in these samples appears to be related to stride-specifics and orientation of centre of mass prior to touch-down. Maintenance of balance from stride-to-stride requires at least partial compensation at ground contact, especially in the long-limbed ostrich with a high centre of mass. Based on variations in standard deviation values among ground contact elements, this corrective function appears to be largely the responsibility of the 4th toe.

The participation of the 4th toe at ground contact is likely determined by a combination of direct muscle control, response to ground conditions and reaction to fluctuating load-bearing demands based on overall body posture. Identifying the actual impetus behind 4th toe position and load-bearing becomes even more challenging when viewed within the confines of the automated 4th toe ab-/adduction sequence as dictated by limb morphology.

Until further research is undertaken in this area it is fair to postulate that, regardless of cause or origin, the 4th toe is the only phalangeal element in the didactyle ostrich capable of acting in direct compensation to substrate conditions or to obviate potential imbalances in CoM. This responsibility is clearly illustrated in the consequential relationship of 4th toe position to LD and CoP at touch down and explains, to a great degree, the variability in the J-shaped CoP path during the first 33% of ground contact. Subsequently, CoP path follows a typical latero-medial shift with movement of the CoP towards – and subsequently through – the longitudinal centre of the immutable 3rd toe.

It would be fair to state that, without the 4th toe and its ability to provide moment-by-moment fine adjustment for CoM, an ostrich moving at relatively slow speeds would experience notable challenges in the maintenance of balance. Running samples indicate higher consistency in LD and CoP path and thus a potentially less important compensatory role for the 4th toe in straight running at speed.

Walking versus running

The relatively greater variation in SD in walking compared to running samples was to be expected. Especially during very slow walking, stability must be maintained *via* consistent nervous control to effect muscular corrections of the upper limb and 4th phalangeal element. At running speeds of 3 to 6 ms^{-1} these compensatory mechanisms are not required to the same degree. This was reflected in the maximum values of LD for all ground contact elements which fell within a relatively short time frame indicating that 3rd toe, claw and 4th toe function more in the manner of a single entity at higher speeds. It can be expected that, as speed increases, SD would decrease further and reach an absolute low during high-speed running. Within this context it is important to note that – as an adaptation towards efficient running performance – articular motion range throughout the pelvic limb is constrained to a high degree by passive structures (Firbas & Zweymüller, 1971; Fuss & Gasser, 1992). This results in a concentration of limb motion in the fore-aft plane with very limited mediolateral excursion of the distal limb. Only the knee exhibits a wider range in degrees of freedom with a maximum ab-/adduction range of 45° to allow a certain bracket of proximal adjustment for management of CoM. Combining these morphological presets with the effects of dynamic stability, phalanges are largely directed by external forces and are relied upon simply to ensure proper ground contact and substrate traction *via* the claw without great diversion of energy for the application of neural or muscular control. Indeed, there is little time for positional compensation considering the short GCD at a duty factor of 0.29 when running at 60 kmh^{-1} (Alexander et al. 1979). This hypothesis gains weight when assessing the ground contact elements separately: SD of the rather constrained 3rd toe is the lowest at all speeds, while the relative standard deviation in 4th toe maximum load bearing is as high as 70% in walking compared to 35% in moderate speed running.

Degree of metatarsophalangeal joint flexion is reflected in load distribution

The proximal part of the 3rd toe (essentially the “heel” of the “foot”) bears considerably higher loads in running than in walking. This is the result of the increased metatarsophalangeal joint flexion that occurs during running and is confirmed by our video analysis. The metatarsophalangeal joint is minimally flexed in walking but undergoes high flexion during running to the degree that it nearly contacts the substrate at mid-stance. This observation corroborates the proposition that the metatarsophalangeal joint is the primary reservoir of elastic energy storage and reflection in the ostrich. This role is complemented by the intertarsal joint that remains in a nearly fully-extended state during GC in moderate and high-speed running to ensure that load is effectively channelled into the metatarsophalangeal joint complex (Rubenson et al., 2007; Schaller et al., 2005). Consequently, we recommend that any study of this type be undertaken with ostrich specimens that clearly employ the natural supra-jointed toe-posture seen in healthy, active animals.

High phalangeal loads do not appear at the distal phalangeal elements and are instead focused towards the “heel” of the 3rd toe – and consequently into the shock-absorbing metatarsophalangeal complex – to reduce the need for muscular stabilization. High moments concentrated at the metatarsophlangeal joint result in a more efficient/economic stance since high moments acting distally would require counteraction through the exertion of additional muscle force and/or skeletal structures, increasing overall energy demands. It can be assumed that the moments acting on the metatarsophalangeal joint at higher speeds represent a beneficial proximal shift of load to minimise muscle work during the costly stance phase (e.g. Ellerby & Marsh, 2006).

Claw as positional anchor

At high speeds, a significant increase in load resulting from the inertial mass of the accelerated body is concentrated on the phalanges within a short time-frame. To manage these forces, the downward curving claw is embedded in the substrate to provide a positional anchor during ground contact and provides an additional propulsive lever at toe-off. A cross-section of the claw renders a triangular shape, with the leading point of the triangle oriented cranially. In the lateral view, the claw is undercut at a 45° angle to form a sharp point at its distal end. This profile permits bayonet-like entry of the claw into the ground, excellent resistance to dislocation once embedded and provides a straight segment of the triangle perpendicular to the vector of force application during propulsion to maximise force transference through to the substrate.

The increasing participation of the claw at higher speeds is driven to a certain degree by an anatomical precondition. In our manipulation experiments with an isolated lower ostrich limb with intact tarsometatarsus and phalanges, the toes were placed on a flat surface with the tarsometatarsus oriented vertically and increasing pressure was manually applied through the long axis of the tarsometatarsus. With little or no pressure exerted, the claw remained slightly above-grade and did not contact the substrate. Once subjected to an energetic thrust, the claw contacted the substrate and simultaneously moved into a more pronounced downward-facing position in preparation for ground penetration.

Naturally, the load-induced claw-push is actively enforced by the high power output of the toe flexors during stance phase in running which flexes the toes more than during walking, creating a slight arch between the proximal and distal pads of the 3rd toe. This is reflected in the shorter measurements of maximum length from claw-tip to the end of the proximal 3rd toe-pad in running samples when compared to walking. At slower speeds on solid substrate, when duty factors are well above 0.5, the ostrich does not rely on the claw as a positional anchor as indicated by low load-bearing values.

As an offshoot to purely scientific inquiry, these findings may be applied to current ostrich farming practices in certain countries that involve amputation of the claw to reduce the likelihood of damage to the skin of other birds in the flock – later used in leather production. De-clawing would significantly alter locomotor behaviour and could result in a reduction of flock health arising from reduced running activity.

4th toe fine-tuning

One might argue that the 4th toe is essentially a vestigial appendage that contributes no active correction for CoM and that variations in load are simply a random consequence of a particular body posture with a given limb placement. Indeed, further evolutionary reduction of the 4th toe in the ostrich persists as a topic of debate.

This suggestion is contradicted by the simple fact that peak loads for the 4th toe fluctuate over a wide range. It is thus reasonable to conclude that these fluctuations are related to the maintenance of balance. High variation in load is probably a consequence of the fixed position of the toe once placed on the ground, resulting in the employment of toe flexors to modulate pressure on the substrate to achieve solid stance and actively avoid imbalance. Simply stated, if the 4th toe were a vestigial appendage, we would not expect to see such a great degree of participation during stance, nor would we expect such a high standard deviation in load. Although movement is limited to only 6° medially and laterally beyond mean angle, the 4th toe has a wider range of motion in the vertical plane, presumably to compensate for uneven ground conditions or obstacles. 4th toe position relative to the 3rd toe is established immediately upon touch-down with no indication that positional corrections are executed to manage CoM. However, the linear inter-dependence of CoP origin and phalangeal LD suggests function of the 4th toe as a stabilising “outrigger” with high compensatory qualities that are less related to actual position than to an ability to instantly modulate load-bearing capacity despite its small ground contact surface area. This hypothesis is supported by the fact that 4th toe peak load in walking occurs at the initial 1/3 of GCD when corrections to – and support of – CoM are typically required in response to substrate conditions, body posture resulting from the previous stride or external conditions like wind, jostling from flock partners or small changes in ground elevation. A final point against further reduction of the 4th toe might be supported by the consistent establishment of the tripod-like “footprint” at ground contact in running and the resultant general increase in Base of Support (BoS) in this didactyle bird.

CoM management

Achieving stability while standing and during slow locomotion is obviously more challenging for bipeds than quadrupeds which possess increased static stability attributable to their distribution of ground contact elements and more substantial BoS. Even the other large ratites still possess three toes with a grounded metatarsophalangeal joint providing a comparatively larger BoS. For example, our comparative analyses showed that the rhea (*Pterocnemia pennata*) has a 75% larger GCS than the ostrich relative to body mass (unpublished data).

The didactyle ostrich must ensure that its CoM always moves through the relatively small triangle of ground contact surfaces consisting of 3rd toe's proximal end, 3rd toe claw and 4th toe tip as the major points of load-bearing in running. Tuning of 4th toe position and modulation to load-bearing are required to influence CoM location during locomotion, especially since the CoM is located approximately one metre above ground (e.g. Rubenson et al., 2007). CoM is positioned on a horizontal axis between hip joint and distal femur/knee and typically shifts along this longitudinal axis in the fore-aft plane with nearly no lateral displacement due to a stringent pelvic architecture featuring an interacetabular distance that is relatively the smallest amongst all avian species (Firbas & Zweymüller, 1971). With CoM elevated so far above-ground, slight modulations at the 4th toe would have pronounced impact on CoM.

This effect is more significant at walking speeds where the maintenance of balance is absolutely dependent on active CoM management (e.g. Hof, 2008). In running, the effects of dynamic stability and compensation to CoM *via* wing participation reduces the demand for fine adjustment at the 4th toe, thereby allowing energetic input to be focused primarily towards fast locomotion.

Perspective

In order to derive a uniform data set for use in our analysis scheme, this study focused on obtaining samples of straight walking and moderate-speed running and disregarded incline and decline situations and acceleration and deceleration events. With this solid database of straight walking and running samples, it would certainly be interesting to expand the inquiry by adding variations to the performance set-ups. This would include high-speed running in the 17 ms^{-1} range and execution of 90° - 180° turns to investigate 4th toe function and claw anchoring in more detail under these extreme conditions. However, particularly in fast cutting manoeuvres, the wings are employed as an active component of terrestrial locomotion. We have, on numerous occasions, observed our specimens running within the 6400 m^2 enclosure with estimated speeds of 10 ms^{-1} and performing instantaneous cutting manoeuvres up to 180°, with hard evidence of these events preserved in fresh snow track-ways. In consideration of the strict limitations to degrees of freedom in the hind limb, our observations confirm that this type of manoeuvre is only possible with the addition of wing articulations that enable sudden changes in direction derived from wind resistance. Effects arising from use of the wings would need to be incorporated in subsequent comprehensive analyses since it has been previously illustrated that wings are periodically incorporated in avian terrestrial locomotion (Dial, 2003).

In future inquiries, an ideal set-up would include pressure plate recordings of sequential footfalls of left and right phalanges in a complete stride cycle and inclusion of a set-up where the 3rd and 4th toe contact ground on different levels to render further insight into the compensatory qualities of the 4th toe. Pooling data from a wider array of locomotor conditions would contribute to a more complete understanding of phalangeal function in the ostrich. Additionally, force plates should be included to quantify exact ground reaction forces in parallel with relative pressure data.

Finally, the pressure plate and Footscan analysis technology used in this study proved very useful for determining phalangeal inter-relationships and extrapolating results to identify locomotor strategies that enhance locomotor performance in the ostrich. Employment of this technology in similar examinations of other large ratites would further increase the understanding of toe function in extant cursorial avian species and perhaps contribute to projections of theropod dinosaur locomotion in combination with static analyses of ratite track-ways.

Conclusions

Area of CoP origin is more dispersed in walking than in running presumably due to a lack of dynamic stabilisation effects at slower speeds. Variation in CoP origin results from the greater requirement for fine adjustment of 4th toe position and degree of flexion to manage load and CoM in response to ground conditions and overall body posture at walking speeds. However, there is little divergence from a predictable CoP path and its relative duration at both walking and running speeds once the toes are firmly positioned on the substrate. This consistency is probably dictated by morphological constraints to lateral degrees of freedom that stabilise the entire leg during the latter phase of ground contact. Despite considerations of a possible evolutionary reduction of the 4th toe, its important role as an outrigger for balance in walking and as a significant load-bearing element in running render this outcome highly unlikely.

In running, the increased load resulting from accelerated body mass is directed *via* increased toe flexion to the formation of a distinct tripod-like toe print with proximal 3rd toe, 3rd toe claw and 4th toe-tip supporting the majority of load while proximal 4th and distal 3rd toe are minimally involved. This provides increased stability and establishes function of the claw as an important positional anchor during ground contact at speed. The claw's defined triangular cross-section limits slippage in all directions once embedded in the substrate and full participation of the claw in all phases of ground contact at higher velocities confirms its use as both anchor and additional propulsive lever at toe-off.

The relatively high loads measured on the proximal part of the 3rd toe in the first 33% of GCD in running indicate a load management strategy that focuses elastic energy storage in the flexor tendons of the elevated metatarsophalangeal joint.

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4.3 Contributions from a non-locomotor element

4.3.1 Wings

Obviously, the hind limbs are entirely responsible for propulsion in the cursorial ostrich. The flightless status and exceptional running ability of this terrestrial bird has understandably focused attention away from its wings, leading to a general disregard of a potentially important contributor to locomotor efficiency. Wings are engaged to varying degrees in a range of behaviours during all locomotor modes. It has been previously proposed that the wings act as “air rudders” to compensate for the stringently constrained articular motion range of the hind limb in turning manoeuvres (Schaller et al., 2005). Acknowledgement of the important role played by forelimbs in studies concerning human bipedal locomotion provide evidence that arm motion is neurally coupled to leg cadence and that swinging the arms fulfils an important stabilising role (Dietz et al., 2001; Vanemerik et al., 2006). In an interesting study on non-conventional wing use in birds, Dial (2003) found that adult and sub-adult galliform birds “...use wing-assisted incline running (WAIR) to enhance their locomotor performance through improved foot traction…”, essentially employing the wings to increase and maintain ground contact as opposed to a more typical use towards achieving flight.

It is commonly acknowledged that ostriches use their wings to protect chicks from excessive sun and rain, for display in mating, to “splash” themselves with sand and other particle manner to groom skin and plumage and to regulate body cover as an important component in thermoregulation (e.g. Sambraus, 1994; own observations). It has also been proposed that forelimb articulation is used as a form of intra-specific communication (personal communication U. Braun).

In the course of this study, it has been observed that the wings consistently participate in walking and running gaits with the degree of wing ab-/adduction modulated in relation to locomotor behaviour. The wing skeleton is relatively long (~ 67 cm) when compared to other ratites, featuring a humerus as long as 43 cm with ulna and radius amounting to approximately one-third of humerus length (Bezuidenhout, 1999). In live specimens, the surface area is greatly increased by plumage consisting of various feather types with the most prominent feathers – the quills – often featured in fashion products.

To-date, the wings have been either systematically ignored or deliberately functionally eliminated in kinematic studies of ratite locomotion in general and ostrich locomotion in specific, presumably due to their status as flightless. In experiments, this has taken the form of strapping the wings to the body in unnatural positions or removal of primary feathers to allow observation of the pelvic limb. In order to make the hip joint visible, great portions of wing plumage were removed in a study in which juvenile ostriches were engaged to perform slight changes of direction (Jindrich et al., 2007). It stands to reason that functional removal of wings can only render incomplete results not applicable to actual locomotion of intact adult specimens.

In this final work stage, the aim is to introduce the importance of a physical structure not directly involved in propulsion and present anecdotal evidence of the general role of wings in locomotor performance. The following observations are intended to deliver a first estimate of wing involvement in locomotion and suggest a methodological concept for later detailed analyses. It must be understood that these observations are not the result of systematic data gathering but are rather intended to define obvious locomotor behaviours in which fore and hind limb activity appear inter-dependent.

Materials and methods

Video footage and photo documentation of four adult ostriches (two males 13 years of age and two females, three years of age) has been analysed for evidence of wing use within a range of locomotor modes. Video footage was taken in the course of previous kinematic and pedobarographic studies in a corridor described in detail in Chapter 4.2.3. Additional photographs and video documentation were undertaken on numerous occasions over a three-year period of observation of the animals in their enclosure. Valuable action sequences were often documented upon release of the ostriches from their overnight shelter when typical episodes of strutting, running and dancing would occur throughout the enclosure. These sequences would often involve intricate displays of chasing and dominance behaviour, typically accompanied by extravagant use of the wings. The consistency of these playful morning exercises appeared to be an important component of health maintenance and coordination development. A particularly good sequence of photo documentation was obtained after a fresh snowfall and provided the additional benefit of detailed track-way analysis.

Observations and discussion

Ostrich wings are used in terrestrial locomotion not to achieve flight – impossible for the ostrich primarily because of its significant body mass – but rather to manage and direct the two main forces of aerodynamics despite relegation of this animal to the ground plane. The forces of lift and drag are exploited to execute a wide range of manoeuvres that increase the scope of ostrich movement. In the same way that fast cars require excellent brakes, it is unlikely that the ostrich would have developed the capability of reaching speeds up to 80 kmh^{-1} without a suitable method for controlling or arresting its inertial potential. Several examples of wing use are described below.

Turning/cutting manoeuvres

Due to the stringent restrictions in hind limb mediolateral degrees of freedom, ostriches are largely unable to execute small radius turns at running speeds without the use of their wings (**Fig.** 4.3.1.**1**). The primary approach is to use the wing as an air rudder by combining the effects of speed and drag harnessed by the large surface area of the rapidly deployed wing (**Fig.** 4.3.1.**2**). This causes the body to rotate in the direction of the extended wing and can be theoretically compared to the mid-flight adjustments performed by flying birds. For the terrestrial ostrich, this technique requires a slight reduction in traction at the ground surface, with these motions often coordinated with a point in the stride cycle when body mass has a lessened effect on the phalangeal traction surface. Depending on overall speed and the corresponding potential energy available from drag, this method can result in very rapid changes in orientation relative to the vector of travel, including full 180° reversals within a very rapid timeframe.

Braking manoeuvres

In a more extreme example of the general technique described above, an ostrich at speed can swiftly extend both wings to present a very large surface area to arrest forward motion by exerting maximum drag. Interestingly, the wing can be articulated so that the leading wing edge is oriented upwards, causing the ostrich to attain a very erect posture, or with the leading edge facing downward, with the expected opposite result in posture (**Fig.** 4.3.1.**4**).

Modulating lift

Ostriches at full running speed can be observed with slightly elevated wings conforming to the shape of the overall body contour. This results in a space appearing between wing and body and is often coupled with a slightly elevated tail position (**Fig.** 4.3.1.**3**). As seen in third-party video footage, this position will be maintained for the duration of long periods of fast locomotion over level and generally unobstructed ground and may provide a range of functions (e.g. Del Hoyo et al., 1992; Grzimek & Grzimek, 1959).

This wing position would augment the effects of dynamic stability by increasing aerodynamic stability in much the same way that rudder and wings on an airplane prevent excessive roll, pitch and yaw during flight. In intermediate speed running of ~ 3.3 ms^{-1}, pelvic movement on these three axes is already quite contained with roll measured at a mean excursion of 6°, pitch with a mean excursion of 6° and yaw with only 2° of excursion (Rubenson et. al., 2007). At higher speeds, the ostrich torso is increasingly stable on all axes, with propulsive energy very efficiently channelled to movement in the forward direction *via* the legs. Slight adjustments in wing position could be used to manage balance or initiate slight changes in direction without requiring additional control or alteration to stride patterns or phalangeal position. Finally, raising the wings during running would increase cooling effects to manage rising body temperature resulting from extreme metabolic work.

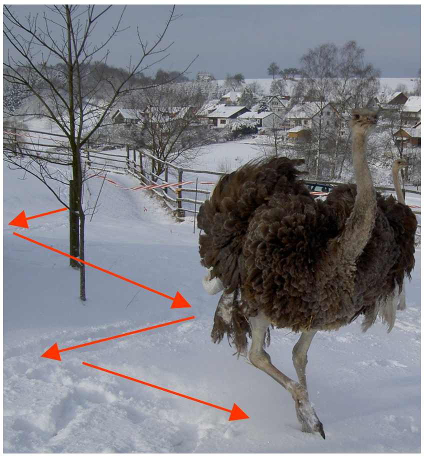

Fig. 4.3.1.**1**: Zig-zagging over a range of ~ 40 m

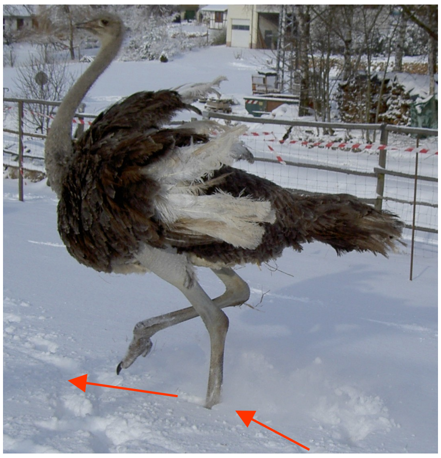

Fig. 4.3.1.**3**: Acceleration with wings and tail lifted

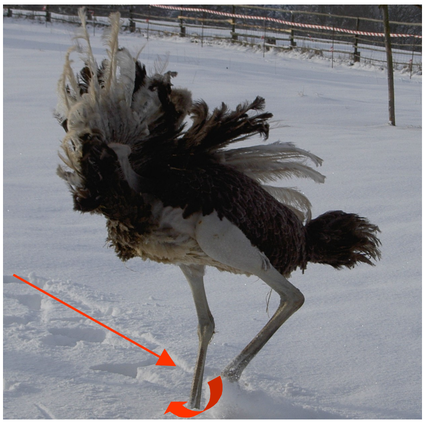

Fig. 4.3.1.**2**: Turning manoeuvre ~ 160°

Fig. 4.3.1.**4**: Braking manoeuvre with limb joints flexed

Conclusions and perspective

As discussed in previous chapters, no part of an organism can be declared "useless" just because an observer is unable to determine its function. This chapter presents a clear instance of an anatomical structure that has been defined as substantially unimportant due to an over-arching definition of the ostrich as "flightless". This definition has perhaps served to obscure the very real contribution made by the wings to the exceptional locomotor performance of this grounded bird. Future studies should first qualify, and then attempt to quantify, the participation of the wings and determine the resultant effects on metabolic requirements and locomotor output before eliminating this factor in the equation of avian terrestrial locomotion.

With the forelimbs appearing to play an essential role in numerous situations, any examination that disregards their impact is, by default, incomplete and may not render accurate functional understanding of the organism as a whole. It should be remembered that other flightless birds are, to varying degrees, also dependent on their wings. Perhaps the most extreme example is the penguin (Sphenciformes) which, although unable to run, is able to fly underwater with enhanced speed and manoeuvrability (Baudinette & Gill, 1985).

In the context of wings as appendages for managing balance and manoeuvrability, it is interesting to ask how certain species of the extinct Struthiomimidae – theropod dinosaurs with similar size and locomotor abilities seen in the extant ostrich – managed rapid shifts in direction. With the forelimbs of Mononykus and Alvarezsaurus extremely reduced and unable to provide air resistance, these theropods instead executed controlled turns and modulations to balance using their long tails (e.g. Chiappe et al., 1997; Senter, 2005).

In future attempts to determine the impact of wings on locomotion, air resistance and lift of a prepared wing at a range of angles and wind speeds could be measured in a wind tunnel. Subsequent analysis of the barbule-less feathers, measurement of individual feather types and emphasis on the unique downward-cupped shape at the bottom ridge of the feather might provide further insight into the aerodynamics of these structures.

Analysis of *in vivo* effects might prove more challenging since application of invasive methods and devices may interfere with motion range, speed or willing participation of the ostrich in experiments. A possible solution to this problem could include ostriches running on a treadmill with "ground speed" coupled to wind speed in controlled conditions to measure changes in ground reaction forces as a factor of land and wind speed in combination with wing use. This experiment would provide definitive results pertaining to the net effects of lift in high-speed ostrich locomotion, potentially decreasing "effective mass" of the bird and providing a new and unexpected explanation for locomotor efficiency in the ostrich.

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5 General discussion and integration

Doctoral thesis overview

The preceding chapters have presented a wide range of results across many disciplines. In every case, the basic principles of a given discipline were researched in detail to allow development of an investigative model pertinent to the overall aim of this project. An ever-evolving relationship between principle and applied methodology allowed application of modified techniques and tailored experiments to increase understanding of the structural attributes that contribute to locomotor performance in the ostrich.

This approach was not – and could not be – a linear one. Instead, this course of investigation was deliberately cyclical and predominantly free of the constraints imposed by institutional structures, external benchmarks and preconceived ideals. It started with a simple, direct and ultimately fascinating question: How does the ostrich run so fast for so long? Research was initiated using the classical scientific technique of pure observation of living specimens under natural conditions. Early acceptance that there was no easy answer to the essential question led to the determination that this unique ability is enabled by an array of interdependent sub-systems, each an important piece of a complicated puzzle.

To mirror this reality, the path towards a more complete understanding of this multiplicity of sub-systems required equally diverse streams of inquiry. Identification of components within the puzzle allowed isolation and distillation of elements to determine their contribution in detail, followed by recombination of data and further refinement of perspective on the working whole. In some cases, this process necessitated revisiting and expanding knowledge of certain elements to clarify relevant connections. The freedom to pursue results on an as-needed basis was critical to the successful unfolding of this inquiry and was enabled largely by the independent nature of this research.

It must be stated unequivocally that reaching an absolute, definitive understanding of the interwoven complexities of any living organism remains a great challenge. Although a number of specific doors have been unlocked by the results of this study, a parallel relevance for this work might be found in the actual format of this investigative model, wherein the "attitude" towards the subject favoured an inclusive, multi-disciplinary approach while maintaining an unwavering intent to regard the ostrich as a remarkable and successful inhabitant of its environment.

The individual components of the morphological and dynamic framework explored in this thesis have been positively identified as intrinsic to exceptional locomotor performance and are now added to the "Intersection of Methods" diagram first presented in Chapter 3, Materials & methods (**Fig.** 5.**1**). Contextualisation and integration of these elements in the following pages illustrate the stringent relationships between form, function and manifestation within the living animal.

The statics of equilibrium in the standing ostrich

Before locomotion can be contemplated, an organism must possess the basic preconditions for balance. The ostrich incorporates a range of strategies to maintain balance and stability in accordance with its exclusively terrestrial lifestyle. The long trunk is positioned horizontally – like a beam – on vertical limbs. This orientation provides inherent structural stability and equilibrium in the standing ostrich, especially when considering that the neck and head are comparatively light and exert a negligible counterweight effect on this basic arrangement between trunk and limbs. The fundamentally straight-axis extremities result in limb joints that are free of significant flexing or extending moments due to ground reaction forces acting in a vertical vector through to the standing body. As typical in avian species, the femur is oriented horizontally but is relatively short in the ostrich to minimise flexing moments on the hip and knee joints.

The ilium is comparatively long in the ostrich and, with a rigid vertebral column, is adequately braced by muscles, tendons and ligaments to maintain this essential "post-and-beam" architecture. The long postacetabular portion of the ilium provides a significant attachment area for trunk-stabilizing musculature to ensure effectively directed tractive forces to control the short, horizontally positioned femur and, consequently, the distal limb.

When focusing on internal structures, the strongly developed ligamentous system exhibits a variety of passive stabilising mechanisms that "encase" each joint. In particular, the intertarsal joint, located at the junction of the longest segments of the limb – potentially a weak-point in engineering terms – is additionally stabilized by the complex interplay of the structural components of the engage-disengage mechanism (EDM, see chapter 4.2.2). This ensures that the intertarsal joint provides a reliable vertical column in support of the substantial body mass of the ostrich.

In compensation for out-of-balance conditions, the standing ostrich adjusts hip and knee joints but can also "bounce" on its uniquely elevated metatarsophalangeal joint, presenting a fine example of a dual-purpose structure that is advantageous to locomotor dynamics as well as the maintenance of equilibrium. Importantly, the didactyle ostrich has reduced the 2nd toe but retained the 4th toe as a necessary outrigger for the maintenance of balance (see Chapter 4.2.3). As in the human biped, mediolateral balance corrections are effected by sideways steps.

Mechanical preconditions for passive limb support are evident in the cantilevered pulley system formed by osseous protrusions at the proximal tibiotarsus and tarsometatarsus wherein the Crista cnemialis cranialis is elongated in the cranial direction and the hypotarsus is elongated in the caudal direction. This implies that the interconnected muscle-tendon system running over these protruding structures is in a state of tensed equilibrium when the ostrich is in standing position. As with the metatarsophalangeal joint, the Crista cnemialis also plays an important role in locomotion.

Locomotor dynamics in the running ostrich

Preconditions and Variables

Once static equilibrium has been achieved, effective locomotion requires that the underlying morphology of an organism provides structurally adequate bone density, appropriate bone segment shape and suitable inter-arrangement of segments to manage the forces arising from muscle input and impact with the substrate. Muscle power must be sufficient to provide limb segment propulsion and exert segmental control to effect movement in the preferred direction.

With these basic parameters accepted as a given in any functioning cursorial animal, three main variables can be explored to determine potential for speed: power output, stride length and stride frequency. A top performer will exhibit distribution of muscle mass towards the trunk to concentrate power generation within the structural framework of the body, long limbs to maximise stride length and light distal elements to ensure high stride frequency. The metabolic and mechanical efficiency with which those three parameters are managed determine the endurance threshold of the organism.

Within this context, the various structural attributes and dynamic strategies employed in the ostrich stride cycle are presented below with emphasis on the structural attributes contributing to high-speed endurance running.

Latter stage of ground contact and Push-off:

Muscle power transmission is facilitated by the multi-jointed muscle-tendon system functionally connecting pelvis to toes through a mandatorily combined sequence of joint flexion/extension combined with stringent limitations to mediolateral degrees of freedom. Power originating at the pelvic and femoral muscles is concentrated through joint dynamics that express form closure rather than force closure qualities, wherein joint structure guides limb segment orientation and articulation to a much greater degree than active muscle input. This arrangement allows delivery of maximum propulsive force with minimum energy diverted to the management of overall limb positioning. The EDM-stabilised intertarsal joint establishes a solid tibiotarsal/tarsometatarsal column that ensures power transmission through to the metatarsophalangeal joint. The unique elevation of the metatarsophalangeal complex – not seen in any other avian species – provides an extra component of flexion in the kinematic chain to manage shock absorption and establish a reservoir for the storage and reflection of elastic energy, delivering significant impulse as this joint extends to release the potential energy in toe flexor tendons at push-off. The embedded claw provides positional anchoring and a final point of propulsive leverage during the critical final phase of push-off when all power is focused and explosively released through this small ground contact element. Thus, the proximal impulse provided by the powerful hip and knee extensors is channelled through all elements of the limb and ultimately through to the ground with a high degree of efficiency.

After Push-off:

The entire limb now rapidly retracts up and towards the pelvis during flexion, initiating swing phase and effectively elevating the distal limb elements above any obstructions – like long grasses or scrub – that may inhibit locomotor progress.

This is again facilitated by the interconnected muscle-tendon system and includes automatic adduction of 4th toe and toe flexion. The distal limb is now positioned very close to the fast-moving trunk resulting in concentrated mass and reduced wind resistance. During this stage of overall limb flexion, the thrust present during disengagement of the EDM could deliver an additional flexing impulse through the limb and facilitate faster retraction than might be possible in the absence of the EDM.

Swing phase:

As swing phase begins, the limb requires forward re-acceleration to the point that it exceeds the net speed of the body to continue the stride cycle. In any organism that attempts to maintain high running speeds for extended periods of time, protraction must be as cost-efficient as possible. Here again, the multi-jointed muscle-tendon system couples all joints towards concerted limb extension. The elongated Crista cnemialis cranialis provides additional leverage for hip and knee joint extensors – activated by pelvic and femoral musculature – to automatically extend the intertarsal and metatarsophalangeal joints and toes including abduction of the 4th toe. During protraction, the narrow guidance of the limbs – ultimately dictated by the small interacetabular distance – ensures that limb trajectory is optimally managed in preparation for touch-down. The pelvic muscle complex and short femur yield a proximally shifted primary muscle mass while the long, actively swinging part of the limb is very light with dynamic control orchestrated mainly by long tendons (see Chapter 4.1.1 and .2). This ideal combination of proximally originating power generation and extremely long, light swinging elements – including evolutionary reduction of 2nd toe and corresponding musculature – allow the ostrich to effectively move the limb through a wide arc from push-off to touch-down, thus maximising both stride length and stride frequency. This essential combination of factors for efficient limb swinging is compounded by the structurally restricted range of mediolateral joint movement to focus the great majority of power-output to movement in the fore-aft plane. Just prior to touch-down, rapid extension of the intertarsal joint *via* the EDM establishes a braced support column with simultaneous extension of the distal limb and toes in preparation to absorb ground reaction forces arising from the substantial inertial mass of the ostrich.

Touch-down and first stage of ground contact:

Upon ground contact, the embedded claw establishes a stationary “foot” position to ensure that the body travels over a solid anchor point. Load is concentrated at the proximal part of the 3rd toe and reduces moments acting on the metatarsophalangeal joint. Shock absorption is provided by fat pads on the toes and by the multi-functional metatarsophalangeal joint which, by consequence of its role in load management, stores a significant quantity of elastic energy for recycling at push-off. Shortly after touch-down, the intertarsal joint is sustained in the “engaged” state by the EDM to provide essential support for trunk mass while focusing ground reaction forces within the elastic energy storage structures of the metatarsophalangeal complex below. Results suggest that an intertarsal extensor interacting with ligamentous structures at this joint may actually increase the stabilising qualities of the EDM in proportion to load. This system would allow a great deal of axial loading or muscle force to be applied to the limb without risking structural damage as the degree of joint stabilisation is functionally conjoined to force input (i.e. load via ground reaction forces) or muscle power output.

Similar to the effect seen in standing, the interconnected muscle-tendon system interacts with the osseous protrusions of the Crista cnemialis and the hypotarsus causing limb extension to result in automated toe flexion. This coupled action delivers a tripod-like load distribution “footprint” that ensures embedment of the claw, allows balance management *via* 4th toe pressure modulation, places the majority of load at the proximal part of the major 3rd toe and delivers extra overall grip on the substrate.

Torsional moments occurring in the hip joint – which have the potential to cause imbalance at touch-down – are nearly eliminated by the very small interacetabular distance in the ostrich ilium and are additionally compensated for by the prominent ligamentous system at the hip joint. Small interacetabular distance is the primary reason for the very stable, non-oscillating trunk posture typical of the ostrich at high speed.

Inherent disadvantages in ostrich morphology and solutions to challenges

The disadvantage of locomotion on “stilts” and the inherent limb “stiffness” caused by decreased mediolateral joint manoeuvrability are directly compensated for in the ostrich by the crural joints and indirectly compensated for by the wings (see chapter 4.3.1). Ostrich morphology allows increases in the degree of limb joint flexion to expand the range of mediolateral limb segment rotation on the longitudinal axis so that adjustments for the CoM can be accomplished by joint flexion. When turning with flexed limbs, the CoM is closer to the ground plane resulting in an increase of stability in tight radius situations.

If immediate postural compensation cannot be provided by limb joint adjustment, the wings – comparatively large in this flightless bird – can be used to re-establish or modulate balance of the CoM. With the lower limbs highly constrained as a consequence of the dynamics and articulation of ostrich locomotion, the wings can be employed as air rudders to effect sudden changes in direction or can be deployed simultaneously in highly effective braking manoeuvres.

The constraints imposed by the limited range of joint rotation might cause challenges in feeding, preening or other behaviours but are negated by the long, highly flexible neck and light head of the ostrich, allowing a wide range of mobility to accomplish varied tasks.

The primary disadvantage to ostrich morphology and limb dynamics becomes apparent during locomotion up or down an inclined substrate. This environmentally rare condition – due to life on the savannah or desert plain – causes a shift in balance and compromises limb dynamics to the point where overall corrections for maintenance of equilibrium are laborious at low speed and exceedingly difficult at high speed. Similarly, acceleration or deceleration on slippery substrates compromise grip, resulting in a breakdown of the chain of motion that determines ostrich stability. In practical terms, this serves to illustrate that the ostrich has developed its unique and highly effective locomotor system in a planar environment with relatively little variation in ground conditions.

Concluding remarks

This thesis has provided detailed assessment of a range of specialised structures, identified inter-relationships of elements and described underlying preconditions conducive to fast, long endurance locomotion in the ostrich. In these concluding remarks, the principle of eigenfrequency is revisited to provide a final theoretical encapsulation of the results presented by this research.

The foundation for this principle is that any structural mass, when deformed by internal or external forces, possesses a natural resonant frequency that may be consequently expressed by a specific rate of oscillation through the entire structure if subjected to a constant energy input from the deforming force. If this principle is taken to an extreme, eigenfrequency can be highly disruptive. This is exemplified by a tall building that sways to the point of self-destruction due to specific oscillations of the ground during an earthquake, or a glass that shatters when a highly focused sound frequency causes complete dissolution of form. The beneficial characteristics of eigenfrequency can be profitably illustrated using a hypothetical mechanical system wherein a set of seemingly disparate elements of divergent properties are organised and inter-related in such a way that, when set in motion, each element assumes a specific role in the balanced continuation of the cycle of movement through harmonised oscillation with all other elements of the system. This principle incorporates properties of mass, proportion, articulation, structural integrity and the sum of both internal and external mechanical and inertial forces wherein movement throughout the system operates optimally to preserve dynamic equilibrium. In a finely balanced design, this results in maximum efficiency output with minimum energetic input.

In a biological system, these interlaced factors are comprised of the particular dimensions, composition and mass of bones, muscles, joints and soft-tissues forming the “biomechanical” architecture and, thus, the physical basis for the manifestation and expression of kinetic energy. Neural impulses direct the potential energy supplied by the metabolism to provide animation to the architecture. Within a bio-systemic context, the factor of eigenfrequency is primarily expressed in gait selection, wherein certain gaits provide an optimum oscillation of all elements of the body to deliver a harmonised locomotor expression that exploits the inherent properties and inertial dynamics of all elements in the kinematic chain in an attempt to optimally manage the metabolic cost of motion. A concrete example of this principle in humans is the swinging of arms in symbiosis with the stride pattern of the legs – making us a preeminent long-endurance walking organism – and the subsequent harmonic shift of eigenfrequency when transitioning to a running gait, allowing us to cover greater distances while still deriving the metabolic benefits of a body moving in synergy.

Locomotor systems rely on the force provided by musculature to initiate motion, but also harness the potential energy stored in elastic structures like tendons to derive maximum benefit from reflected energies arising from ground reaction forces. Additional sources of non-muscular impetus include the constraint and release of structures by ligamentous systems and the recycling of oscillating energies present in the wobble-mass of an organism, with the latter being a residual effect of the very mass that is being moved. Thus, once motion is established by the musculature, all other elements of the system coalesce to perpetuate motion, with muscle activation providing propulsion and control of elements with the least possible amount of work. The oft-cited ideal – on a theoretical level – would be the realisation of a “perpetual motion machine”. Within the confines of our corporeal existence, this goal likely remains out of reach.

A biological organism attempts to approach this ideal by reducing metabolic energy requirements and evolving a cohesive unity of structures and structural relationships that push the envelope of efficiency in every facet of its existence. The observations, investigations and results presented for the first time within this work have led to the identification of numerous specialisations and structural attributes in the locomotor apparatus of the ostrich that provide biomechanical advantages towards the aim of perpetual motion. These locomotor elements are contained within a harmonised web of sub-systems that achieve a high degree of biological efficiency to allow remarkable integration of this animal with its environment, providing a valuable example of evolutionary and systemic refinement towards a set of exceptional characteristics.

Fig. 5.**1**: Integration

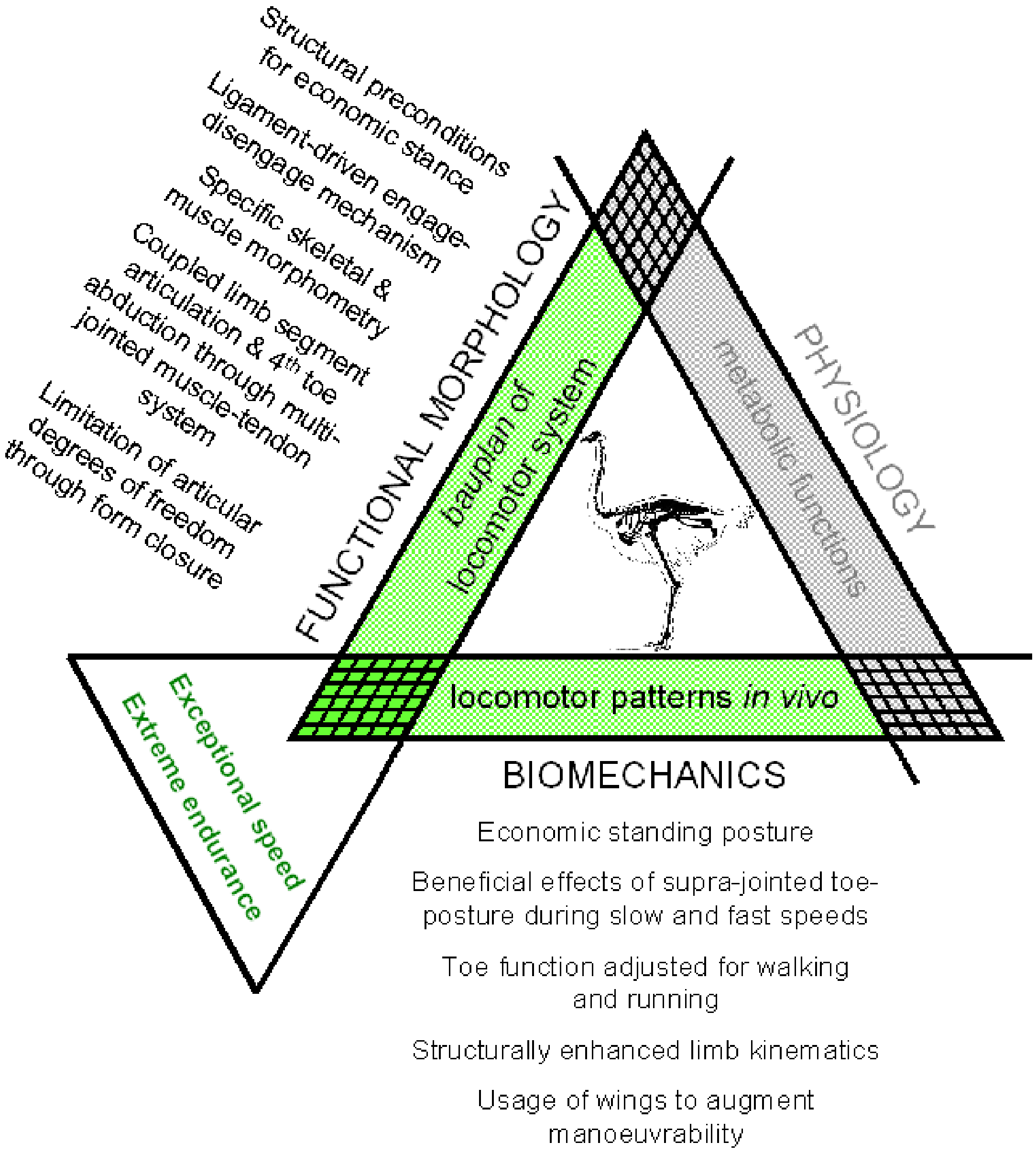
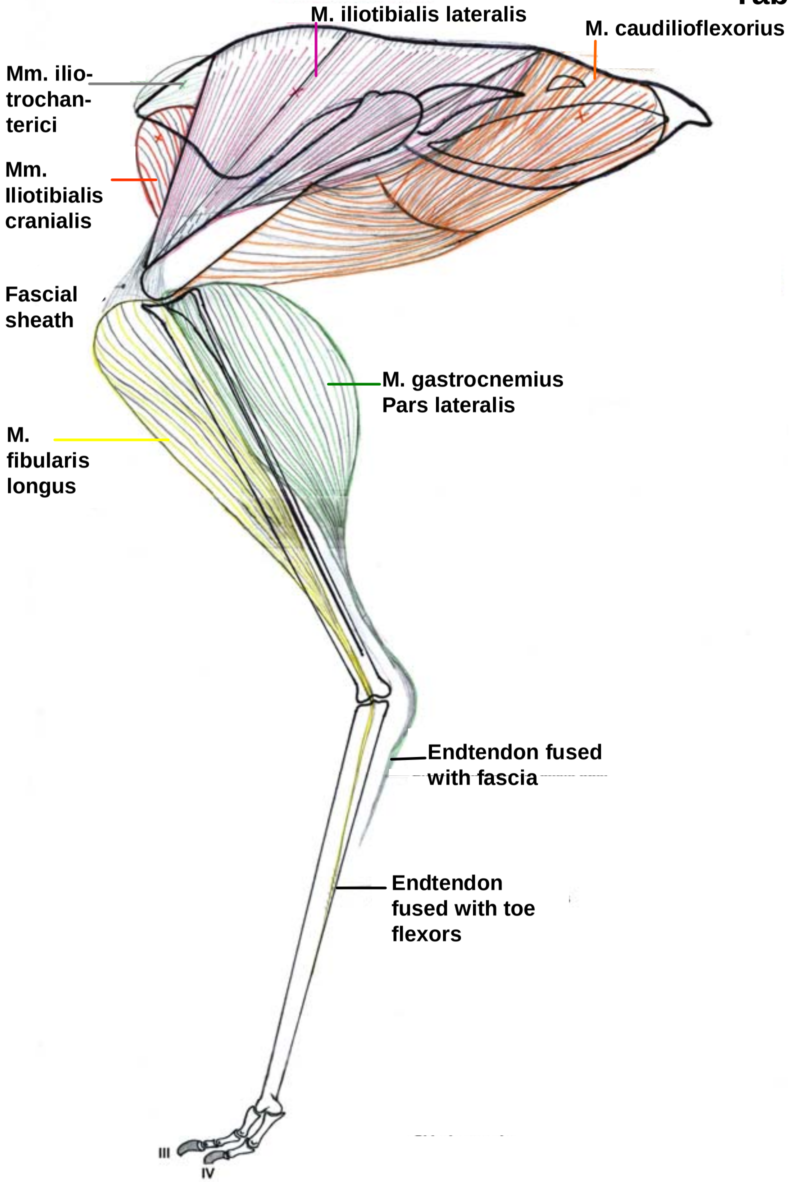
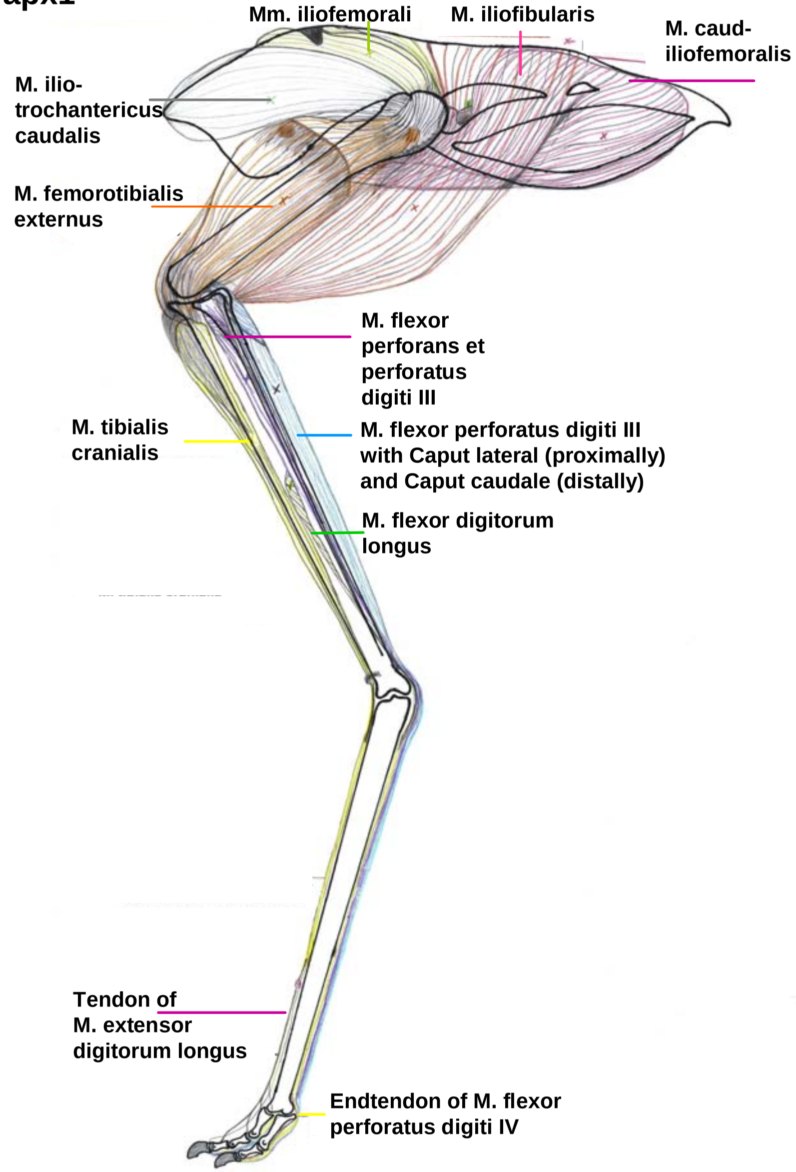


Table apx1

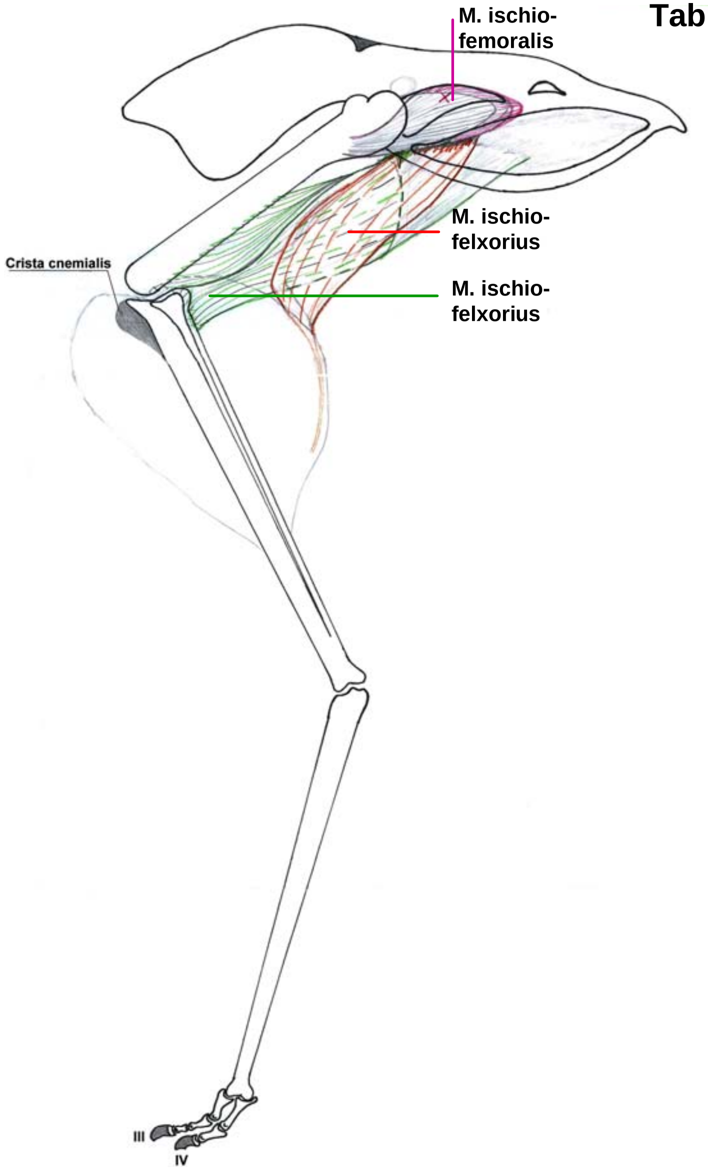


Superficial muscle layer, lateral view.



Lower muscle layer, lateral view.

Table apx2



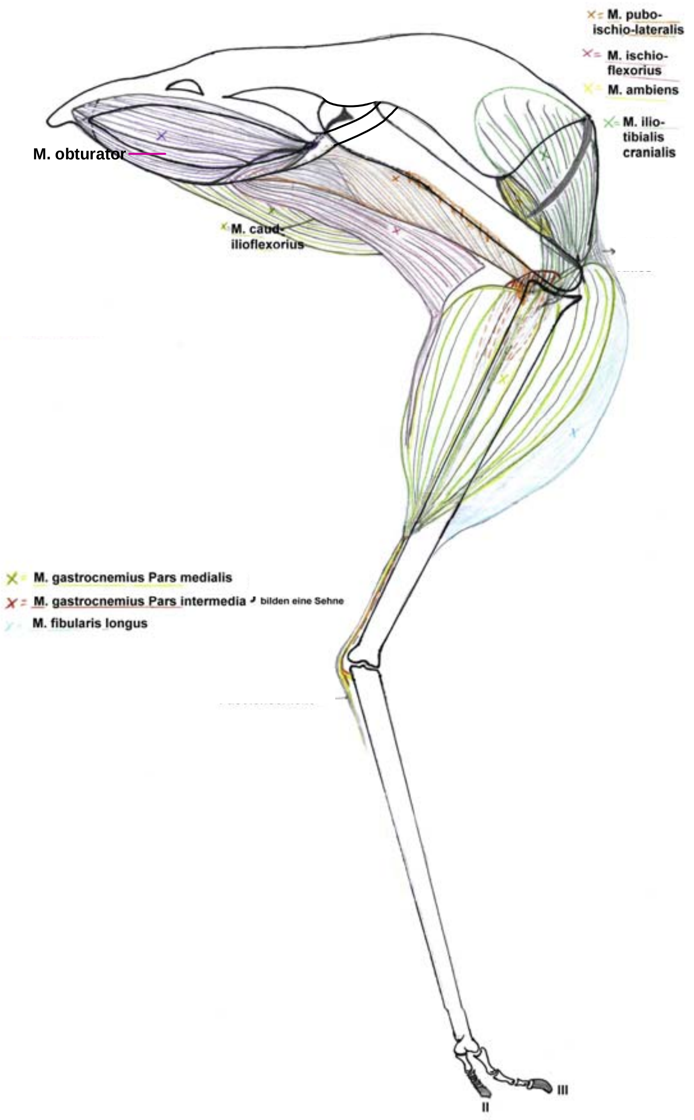
Basal muscle layer, lateral view.

Superficial muscle layer, lateral view.

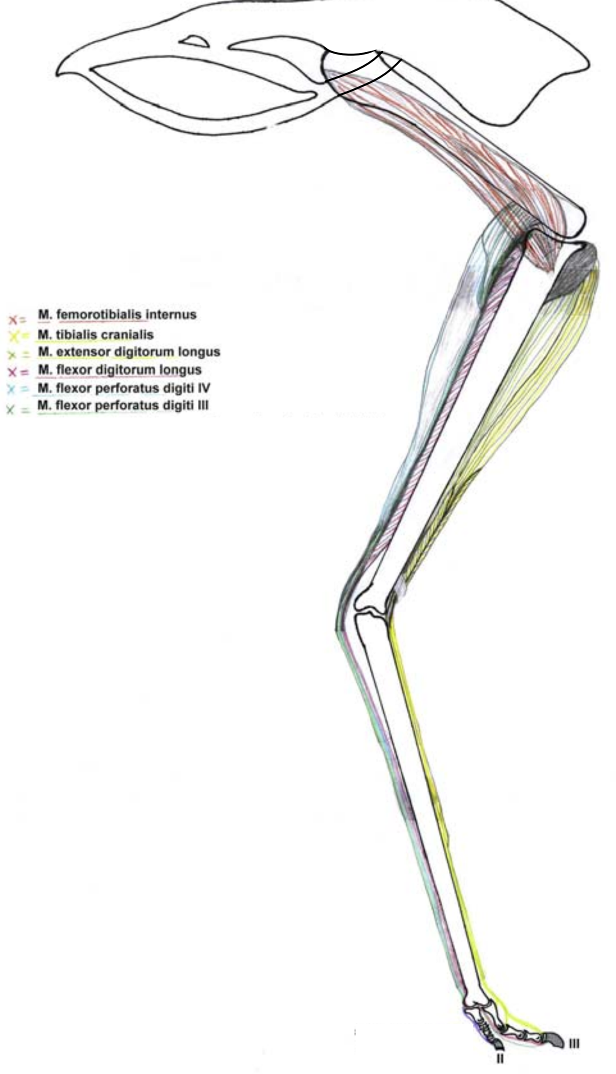
Lower muscle layer proximal limb, lateral view.

Basal muscle layer, lateral view.

Table apx3



Superficial muscle layer, medial view.



Lower muscle layer, medial view.

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