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A9–GENERAL BIOMECHANICS

Organised by A.M. Wilson and J.J. Videler for the Biomechanics Group

A9.1–The relationship between duty factor, sweep angle and speed in the horse during field exercise

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As an animal moves at increasing speed, the angular velocity of the leg relative to the trunk increases at almost the same rate (since leg length is almost independent of speed). If limb angle at foot-on and foot-off was the same at all speeds, then stance time would decrease as a direct function of speed. The angle swept by the limb actually increases with speed (Farley et al., 1993) but the increase is insufficient to fully compensate for the increase in speed, so limb stance time decreases at higher speeds. Limb protraction time is, however, almost independent of speed. Duty factor, therefore, drops and peak limb force rises with increasing speed. We have validated radio telemetry of data from hoof-mounted accelerometers for the determination of foot-on and off, and satellite GPS for determination of velocity. These two systems were then applied to explore the relationship between duty factor and sweep angle as a function of speed and gait.

Data available to date indicate that GRF can be calculated with reasonable accuracy (within 13%) from duty factor assuming that the GRF curve is sinusoidal in nature, as suggested by Alexander et al. (1979) and that gait has little effect on the relationship between sweep angle and speed.

References:

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A9.2–Scaling relationships in the families Suidae and Tayassuidae

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Scaling relationships in animals have generated much interest amongst biologists. Amongst vertebrates, geometric animals have skeletons with linear dimensions that scale proportionally to (area)^{0.5} and (volume or mass)^{0.3}. However, if functional requirements of skeletons are to remain similar across animals of widely dif-

fering body masses, changes in shape of skeletal elements, resulting in deviations away from geometric similarity, are to be expected. The model of elastic similarity, for instance, requires that bone lengths are proportional to (mass)^{0.25} and diameters to (mass)^{0.375} in order that bones deform under gravity in a similar way regardless of size. However, in closely related species, differences in body form may be independent of size and reflect adaptations to habitat or mode of life. The majority of pig species in the family Suidae are forest- or swamp-dwelling species. A few, most notably the warthog (*Phacochoerus adthiopicus*), live almost exclusively on open plains and savannah. In the New World, members of the pig-like family Tayassuidae, the peccaries, are also forest dwelling. Plains-dwelling pigs like the warthog could be expected to show skeletal adaptations that differ from species that live in more closed habitats. We measured length, diameter and least-circumference for the hind-limb bones for eight species of Suidae and two species of Tayassuidae to assess their scaling relationships, and to determine if plain-dwelling animals have skeletal proportions that differ from forest-dwelling species. Data were also collected for a larger group of artiodactyls, perissodactyls and carnivores to allow direct comparisons to be made with a wider group of mammals.

A9.3–The role of biceps in equine locomotion

J.C. Watson, M.P. McGuigan, A.M. Wilson, The Royal Veterinary College, London, UK

Equine biceps have a substantial collagenous component and their muscle fibres are relatively short compared to the length changes that occur during elastic deformation. This suggests that most of the muscle's function is related to its passive properties. Biceps are strained by the downwards movement of the trunk at the shoulder joint. Shortening of the muscle–tendon unit at the end of stance extends the shoulder and flexes the elbow—the movement required to protract the limb. This led us to propose the hypothesis that energy stored in biceps has a role in initiating limb protraction.

Bicep muscles were harvested from horses euthanased for other reasons. Muscle tendon units, approximately 400 mm long, were mounted in a hydraulic jig. Each

muscle was loaded to a force of 8 kN and video motion analysis was used to measure deformation. At 8 kN, the stored energy was 50–57 J and tendon strains were 10%. This is similar to that recorded in other energy storage tendons at peak strain.

Bicep forces were calculated during a trot from shoulder joint moment and limb force using forceplate and motion analysis. The biceps moment arm was determined by radiography. Seventy percent of the shoulder moment was attributed to the biceps. At 85% of stance (when the heel leaves the ground), the peak extensor moment on the shoulder joint was 1600 Nm, producing a peak biceps force of 4.2 kN. The energy stored in the biceps at a force of 4.2 kN is 18 J. If the entire shoulder moment was provided by the biceps, this would rise to 6 kN and 32 J. This is a significant proportion of the energy required to protract the limb.

A9.4—The theoretical limits to the power output of a muscle tendon complex with inertial and gravitational loads

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A muscle and tendon acting on an inertial load can deliver to the load a power greater than could be generated by the muscle alone. This is because energy stored by the muscle in the tendon early in the contraction, when the load is moving slowly, is delivered to the load at a later stage when the load is moving faster and adds to the work generated at that time by the muscle. We term this 'power amplification'. The question we address in this presentation is how much power amplification can be produced by this mechanism. We consider systems in which the muscle is characterised by its force–velocity curve, either linear or curved; the tendon is characterised by its force–extension curve, which may also be linear or non-linear, and where the load is either a pure inertia or a mass subject also to gravitational loading. The methods we have used are dimensional analysis, standard analytical methods to solve the linear cases, and numerical integration for the more complicated (non-linear) examples. In the absence of gravitational loading, the maximum power available is approximately 1.4 times the power output of the muscle alone. With added gravitational loading, this can increase to almost twice the muscle power. The linearity of the force–velocity curve and force–extension curves have only a minor influence on these conclusions. It seems that only cams or catches can further increase the power amplification.

A9.5—Novel muscle activation patterns in the escape response of *Polypterus senegalus*

E.D. Tytell and G.V. Lauder, Organismal and Evolutionary Biology, Harvard University

The kinematics and muscle activity patterns of escape responses in the bichir, *Polypterus senegalus*, were analyzed using high speed video and electromyography (EMG). Five fish were filmed at 250 Hz while recording white muscle activity at five sites on both sides of the body. Body wave speed and center of mass velocity, acceleration, and curvature were calculated from digitized outlines. Six EMG variables per channel were also calculated to characterize the motor pattern. In contrast to previous studies, which observed mostly uniform escape responses, *P. senegalus* shows a wide range of patterns, from very strong responses, in which the head often touched the tail, to very weak responses, with corresponding variation in the length and magnitude of muscle activity. Unlike the classical pattern for escape response muscle activity, strong activity was observed on both the ipsilateral and contralateral sides during Stage I; contralateral activity, however, was significantly weaker and shorter in duration than ipsilateral activity. While simultaneous, bilateral muscle activation, such as we observed in *P. senegalus*, has been hypothesized to increase body stiffness and bending wave speed, we detected no correlation between bilateral activity and wave speed. Escape responses almost always had Stage II contralateral muscle activity, although it was often limited to the two most anterior electrodes.

A9.6—Viscosity rules the wake? Generation, decay and aging of animal generated vortex wakes

E.J. Stamhuis, University of Groningen

Animals transfer momentum to the water when producing thrust. The momentum can be recognized in jets of water, moving away from the animal. Depending on the size of the animal and the induced flow velocities (and hence, the Reynolds number), the vorticity accompanying the jet stays attached or is shed as single or even as series of individually recognizable vortex rings. The results from flow studies conducted in our lab show that the wake structure and the decaying process of wakes changes with increasing Reynolds number (Re). The process of decay of animal generated vortex wakes has hardly been addressed experimentally so far, despite the high ecological importance of wake lifetime with respect to the traceability of a swimming animal by predators and/or conspecifics. Recently, we conducted a series of experiments in which vortex rings were produced artificially over a wide Re range. Several parameters of the vortex rings derived from PIV analysis were followed

in time to map the process of decay. The first results of this analysis will be presented and will be compared to animal generated wakes.

A9.7—Running on water: quantitative flow visualization of bipedal locomotion in basilisk lizards

S.T. Hsieh and G.V. Lauder, Organismic and Evolutionary Biology, Harvard University, USA

Previous work on water surface locomotion in basilisk lizards has focused on limb kinematics and mechanical models of force generation. Nothing is known about the effect of limb motion on sub-surface water flow and the forces resulting from limb impacts. We examined how basilisk lizards (aka 'Jesus lizards') run on water from the standpoint of fluid mechanics, measuring the wake produced by the foot with digital particle imaging velocimetry (DPIV). We induced seven basilisk lizards (*Basiliscus plumifrons*) to run across a water track while filming with two synchronized high-speed cameras. Only data from runs in which the animal ran bipedally (i.e. the front feet did not touch the water) were used in final analyses. Each step was broken down into three phases corresponding with the primary direction of motion of the foot: slap, stroke, and recovery. To assess the shape and orientation of generated vortex rings, we collected data from three different light sheet orientations: x - y plane (parallel to the direction of motion); y - z plane (perpendicular to the direction of motion); and x - z plane (horizontal). DPIV data show that reaction forces from the feet are oriented aft and lateral to the lizard during the stroke, rather than aft and medial, as has been reported for level terrestrial vertebrate locomotion. Analyses include measurements of vortex circulation and calculation of the magnitudes of force generated by the feet in three directions during the slap and stroke phases of a step.

A9.8—Swimming larval and juvenile flounders (*Platichthys flesus*): kinematics and wake

R. Gesser, E.J. Stamhuis and J.J. Videler, University of Groningen, The Netherlands

The flounder (*Platichthys flesus*) is the only flatfish species in the North Sea with larvae migrating into freshwater nursery grounds during metamorphosis. The effects of migration against a salinity gradient and of metamorphosis into the typical flatfish shape on swimming performance are the central interests in this project. The aim of the project was to describe the body kinematics of swimming larval and juvenile flounders in different salinities, to quantify the interactions between fish and water, and to estimate the energetic costs of swimming and ultimately of migration. In contrast to so-

called 'round fish', flatfish lie on one side of their body after their larval metamorphosis and swim by undulating their body and tail up and down. The flatfish morphology and swimming style are, therefore, quite different from round fish.

In the study presented here, metamorphosing larval and just metamorphosed juvenile flatfish at an age of approximately 8 weeks were filmed from the side while swimming freely in still water. Wave characteristics of the undulating body of the flounder, such as amplitude, wavelength, and wave period were derived from these pictures and will be presented, together with our first quantitative data of the flow patterns produced by the animal, resulting from a Particle Image Velocimetry (PIV)-study on larval/juvenile flounder swimming.

A9.9—Novel body kinematics of trout swimming in a von Karman trail; can fish tune to vortices?

J.C. Liao, Harvard University; D.N. Beal, MIT; G.V. Lauder, Harvard University

Flow past cylinders creates a downstream array of staggered, counter-rotating vortices known as the von Karman trail. By altering the combination of flow and cylinder diameter, we can change the frequency at which these vortices are shed. Do rainbow trout (*Oncorhynchus mykiss*) synchronize their swimming kinematics to these vortices, or are they simply drafting in the velocity deficit? If trout are tuning themselves to the frequency of the shed vortices, we expect the tailbeat frequency to be close to the shedding frequency, even as we change the flow speed and cylinder diameter. Our data show that tailbeat frequencies track the shedding frequencies prescribed by the cylinder conditions, while in the absence of a cylinder tailbeat, frequencies are significantly higher. In addition, the swimming behavior of trout behind a cylinder is very different from those of free-swimming trout, undergoing large, periodic lateral translations that we call the von Karman gait. Compared to free-swimming trout, trout swimming behind cylinders have longer propulsive wavelengths, larger posterior body amplitudes, maximum body curvatures that are located more anteriorly, and larger head angles relative to the free stream axis. Preliminary electromyographical data show that trout activate their red muscles during the von Karman gait. These data suggest that trout can actively tune to externally generated vortices. Currently, we are employing Digital Particle Image Velocimetry and a simultaneous high-speed digital video to describe the precise hydrodynamic mechanism of the von Karman gait.

A9.10—Wakes of swimming insect larvae

J.H. Brackenbury, University of Cambridge

Damsel-fly larvae display two kinematically distinct types of escape response: a rapid flex similar to the rapid

C-start of fish; and a more complex twist manoeuvre involving controlled instability in the roll, pitch and yaw planes. Although the preparatory or re-orientational phases of the flex and twist are differently programmed, the second or translational phase, in each case, results in the generation of a thrust jet aligned opposite to the direction of escape. The behavioural, kinematic and hydrodynamic features of these unsteady manoeuvres are discussed in the light of recent findings on the wake dynamics of steady, undulatory swimming in damselfly larvae.

A9.11—Experimental hydrodynamics of locomotion in fishes

G.V. Lauder, Organismic Biology, Harvard University

The technique of digital particle image velocimetry (DPIV) has proven to be a critical method for understanding the function of the fins in fishes. By investigating the function of both median (dorsal and caudal) fins and paired (pectoral) fins during both steady swimming and unsteady maneuvering locomotor behaviors across a broad phylogenetic diversity of fishes, a new picture of locomotor hydrodynamics and the evolution of locomotor function has emerged. Two recent technical improvements in DPIV have contributed new information on the function of fish fins: high-resolution calculation of velocity vector fields using a recursive local correlation algorithm, and stereo-DPIV which allows x , y and z flow components to be calculated within a single planar section of the wake. Comparative DPIV data from sharks, sturgeon, trout, bluegill sunfish, and mackerel illustrate the diversity of fin force production and versatility during steady swimming and maneuvering. Heterocercal tails of sharks and sturgeon differ considerably in hydrodynamic function, despite a generally similar external morphology. Homocercal tails of trout, bluegill, and mackerel all have a mechanical performance (thrust force/total force) of approximately 35%, due primarily to the high lateral forces produced during steady swimming, which average twice the thrust force. The dorsal fin of sunfish produces an actively-generated thrust wake that may augment circulation around the caudal fin and enhance locomotor performance. These data demonstrate the functional versatility of fins in fishes, and the importance of *in vivo* experimental hydrodynamics for elucidating locomotor function.

A9.12—Fast-start performance: morphology and behaviour

P. Domenici, (IMC, Torregrande Italy), C. Brönmark and H. Turesson (Lund University, Sweden)

Most fish species exhibit fast-start manoeuvres in escape responses when attacked by predators and fast-start performance should, therefore, directly affect survival of prey. Past studies on different species of fish have

attempted to correlate fast-start performance with morphology. Based on theoretical considerations, it was suggested that specialization for fast-start performance should include a deep body, a high percentage of anaerobic musculature and high axial flexibility. Previous work also shows that expectations based on morphology have sometime failed to predict fast-start performance, due to behavioural modulation. In addition, previous work has mainly been based on interspecific comparisons, and thus involves phylogenetic constraints. Here, we have analysed the fast-start performance of two morphs of one species, the crucian carp *Carassius carassius*. The crucian carp is a cyprinid commonly found in lakes and ponds. Previous studies have shown that the presence of pike induces a phenotypic change in the crucian carp morphology, resulting in a relative increase in body depth. This morphological change was suggested to be an induced morphological defence against predation by a gape-limited piscivore. In the present study, we test the hypothesis that such intraspecific differences in morphology may also lead to an increase in fast-start performance, according to the idea that a large body depth should improve swimming performance in unsteady manoeuvres. Distance travelled, maximum speed and acceleration were compared between the two morphs. In addition, a comparison of the turning rates during the first muscular contraction (stage 1) was made in order to investigate its potential effect on swimming performance.

A9.13—Fast muscle function in the European eel (*Anguilla anguilla*, L.) during aquatic and terrestrial locomotion

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Eels are capable of locomotion both in water and on land using undulations of the body axis. Axial undulations are powered by the lateral musculature. Differences in kinematics and the underlying patterns of fast muscle activation are apparent between locomotion in these two environments. The change in isometric fast muscle properties with axial location was less marked than in most other species. Time from stimulus to peak force (T_a) did not change significantly with axial position and was 82 ± 6 ms at 0.45 *BL* and 93 ± 3 ms at 0.75 *BL*, where *BL* is total body length. Time from stimulus to 90% relaxation (T_{90}) changed significantly with axial location, increasing from 203 ± 11 at 0.45 *BL* to 239 ± 9 at 0.75 *BL*. Fast muscle power outputs were measured using the work loop technique. Maximum power outputs at $\pm 5\%$ strain using optimal stimuli were 17.3 ± 1.3 W

kg^{-1} in muscle from 0.45 *BL* and $16.3 \pm 1.5 \text{ W kg}^{-1}$ in muscle from 0.75 *BL*. Power output peaked at a cycle frequency of 2 Hz. The stimulus parameters associated with swimming generated greater force and power than those associated with terrestrial crawling. This decrease in muscle performance in eels may occur because, on land, the eel is constrained to a particular kinematic pattern in order to produce thrust against an underlying substratum.

A9.14—The chemical composition, geometric and mechanical properties of immature bone in the fowl

R.H.C. Bonser, Silsoe Research Institute; and A. Casinós, University of Barcelona

We are undertaking an investigation of the mechanical and geometric properties of domesticated birds. Humans have selected for various production traits in birds and it has been suggested that birds' skeletons now depart from an 'optimal' design; such divergence may cause an increased incidence and prevalence of skeletal pathologies. By identifying 'optimal' bone properties and geometry, phenotypes having skeletal design 'deficiencies' will be identifiable.

We present data on regional variation in the geometric and mechanical properties of bone from the humeri and femorae of immature fowl (*Gallus gallus*). We assess the mechanical competence of bone, as determined by Vickers microhardness testing, and bone cross-sectional geometry at the mid-diaphysis and at the distal and proximal epiphyses from IMAT analyses of photomicrographs from each region. We discuss the implications of these regional properties in relation to the functioning of the whole bone.

A9.15—Biomechanics of a shallow diver, the green turtle: variable descent and ascent rates as an adaptation to changes in lung volume and buoyancy

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The green turtle, *Chelonia mydas*, is an air-breathing marine reptile, which submerges with inflated lungs. This relatively shallow diver rarely dives much deeper than its depth of neutral buoyancy. Hence, one of the major factors altering its buoyancy and energetics underwater is the volume of air contained in its lungs. This study aimed at investigating how green turtles optimise their underwater behaviour in order to minimise their energetic expenses. To model the influence of buoyancy on the descent and ascent rates of dives, we continuously monitored the diving behaviour using high resolution

Time–Depth-Recorders (TDRs). Our model predicts the evolution of lung volumes during a dive in accordance with Boyle's Law of gas compression, whereas Archimedes' Principle is followed to estimate the intensity of the buoyant lift generated by the lungs. We discuss the recorded descent behaviour in the light of changes of lung volume and buoyancy with depth. The study shows, for example, that during a dive, turtles adopt relatively faster descent rates when within the high buoyancy zone (i.e. upon leaving the surface), as compared to zones of smaller buoyancy. During ascent to the surface, our model suggests that even though turtles may benefit from the buoyant lift of their expanding lungs (in order to reduce transport costs), there may also exist behavioural adaptations that will directly influence the ascent rates.

A9.16—Architecture, ultrastructure and folding of a beetle wing

R.J. Wootton, I.C. Hunt, C.W. Smith, K.E. Evans, University of Exeter; F. Haas, University of Ulm

The complex morphology of the hind wing of the beetle *Pachnoda marginata* Kolbe reflects the complexity of the mechanisms by which it unfolds for flight, and folds under the protective elytra at rest. Extension and unfolding appear to be driven by the antagonistic action of two direct wing muscles (Haas and Beutel, in press), pulling apart two strong longitudinal veins in the basal half of the wing and initiating a cascade of linked mechanisms in the distal and posterior areas of the wing. Folding reverses these mechanisms, and is driven by active brushing movements of the abdomen (Haas et al., 2000). The role of cuticle elasticity within the wing in the folding/unfolding process needs clarifying. Using mechanical testing and investigation of the cuticle ultrastructure, we examine the possibility that some of the sclerotised cuticular plates within the membrane act as stiff springs, imparting bistability to the wing in the folded and extended positions.

Haas F., Gorb S., Blickhan R. (2000). The function of resilin in beetle wings, Proc. R. Soc. Lond. B 267, 1375–1381.

A9.17—A quantitative analysis of vibration and sound in a physical model of the avian syrinx

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Communication by sound is important for birds, but due to experimental difficulties the physical phenomena underlying avian vocalization are still not well known. The principle sound-producing organ is the syrinx, located at the base of the trachea. This sound generating system is unique to birds and exhibits an immense

morphological variation. This vocal system contains membranes, trachea, bronchi, associated muscles and airsacs. We developed a physical model of a simplified non-oscine syrinx, consisting of a metal tube with one latex membrane in the casing. This model allows much more detailed measurements on membrane vibrations (laser Doppler vibrometry), pressure fluctuations, and flowfield (particle image velocimetry) than would be possible in live birds or in situ on excised syringes. Results show that the fundamental frequency and harmonic stack of the membrane vibrations exactly match those of the sound produced by the model. The fundamental frequency of the produced sound is affected by tube length, but not according to straightforward whistle or resonance theories, as applicable to flutes. Also, the tube width, the density and tension on the membrane effect the fundamental frequency in a complex manner.

A9.18—The effect of Ca^{2+} concentration on Sr-Ca^{2+} pumping in toadfish swimbladder muscles fibres

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Sarcoplasmic reticulum- Ca^{2+} (SR- Ca^{2+}) pump blockers (TBQ and CPA) have been used to block SR-ATPase activity ($\text{ATPase}_{\text{SR}}$) in various skinned muscle fibers, permitting the direct measurement of crossbridge ATP turn-over [$\text{ATPase}_{\text{crossbridge}}$]^{1,2}. However, there was no satisfactory way to block $\text{ATPase}_{\text{crossbridge}}$ permitting direct measurement of $\text{ATPase}_{\text{SR}}$. Recently, BTS (*N*-Benzyl-*P*-Toluene Sulphonamide) was shown to inhibit actin activated ATPase of muscle myosin II, suppressing force in μM concentrations^{3–5}. Toadfish swimbladder muscle is one of the fastest vertebrate muscles, providing a pre-eminent model to study extreme adaptations in the molecular mechanisms of contraction and relaxation. We hypothesized that BTS could be used to block $\text{ATPase}_{\text{crossbridge}}$ in skinned swimbladder muscle fibers. At 25 μM (~1000-fold lower than BDM concentrations²) BTS virtually eliminates force and $\text{ATPase}_{\text{crossbridge}}$, but has no effect on $\text{ATPase}_{\text{SR}}$. We used BTS to make some of the first direct measurements of $\text{ATPase}_{\text{SR}}$ over a physiological range of calcium concentrations (pCa 7.2–pCa 5.2). Curve fits indicate that SR- Ca^{2+} pumping has much lower Hill coefficients than crossbridge force generation.

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A9.19—The effect of impaired thyroid function during development on the mechanical properties of avian bone

R.H.C. Bonser, Silsoe Research Institute; K.E. Deaton, C.M. Bishop, P.J. Butler, University of Birmingham, UK

Thyroid hormones show fluctuating levels during the post-hatching development of birds. We report the results of the first mechanical tests to quantify the effect of hypothyroidism, during post-natal development, on the skeletal properties of a precocial bird, the barnacle goose (*Branta leucopsis*), as determined by microhardness testing. The effect of hypothyroidism is tissue-specific: bone from the femorae of birds is not significantly affected by induced hypothyroidism; however, there is a strong positive relationship between the levels of circulating thyroid hormones and the mechanical properties of bone from humeri.

In the barnacle goose, the development of the wing skeleton and musculature depends on an increase in circulating thyroid hormones. Our analysis shows that, in its absence, the mechanical competence of the bone mineral itself is reduced in addition to the decreased bone length and muscle development previously reported in the literature.

A9.20—Daddy-long-wings, ultrastructure and mechanics of the wing of *Tipula* spp (*Diptera*, *Tipulidae*)

R.J. Wootton, I.C. Hunt, C.W. Smith, K.E. Evans, University of Exeter, UK

Tipula, the common crane fly or daddy-long-legs, provides a familiar example of a wing type which twists through very large angles between up- and down-strokes, delivering weight-support in both halves of the wing beat cycle. Wing structure is superficially simple, but subtle in detail: veingometry, membrane relief, and ultrastructure. We use fine morphology, electron microscopy and mechanical testing to investigate the relationship between design and functioning.

A9.21—Validation of a GPS data logger for determining speed during locomotion

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Accurate determination of speed is important in many studies of human and animal locomotion. This is easily achieved during treadmill exercise; however, during over-ground locomotion and under field conditions, methods are limited. GPS has the potential to provide instantaneous speed measurement and differential systems have been shown to provide accurate data [Terrier et al. (2000) *J. Biomech.* 33, 1717–1722]. Miniaturised

receivers are now available and have immense potential in applications that were previously discounted due to the size and weight of the apparatus. The accuracy of these systems is, however, unclear, with manufacturers reporting velocity accuracies of 0.1–0.2 m s⁻¹. This study set out to validate a non-differential GPS system as a means of determining speed under various conditions.

A bicycle was ridden around a track at 10, 15 and 20 km h⁻¹, and instantaneous speed was determined and logged by a helmet-mounted GPS receiver. Actual speed was measured by a bicycle speedometer. Comparisons of actual speed with GPS speed were made. The effect on GPS accuracy of satellite number (through shielding of the receiver), speed, position dilution of precision and whether on a bend or straight was evaluated.

The mean speed measured by the GPS was 0.063 m s⁻¹ lower than the actual speed. The mean random error was 0.16 m s⁻¹ and 50% of the values were within 0.12 m s⁻¹. The accuracy of speed determination was preserved even when the positional data was degraded due to poor satellite number or geometry.

A9.22—The architecture of the digital flexor muscles of the equine forelimb

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The function of the equine forelimb digital flexor muscle/tendon unit is energy storage during the stance phase and flexion of the carpus and digit. Recent data suggest that they also act as dampers of high frequency vibrations occurring during foot impact.¹ Only limited data exist for fibre length² and physiological cross-sectional area.¹ More detailed information is vital for modelling the mechanical function and role of these muscles.

Digital flexor muscles from equine cadaver forelimbs were dissected and fibre length was assessed in ultrasonographic, macroscopic and microscopic examinations. Preliminary data confirm that the superficial digital flexor muscle is short fibred and rich in connective tissue, with fibre lengths ranging from 4 to 8.5 mm. The deep digital flexor muscle consists of three heads: the humeral head can be divided into three subdivisions, of which one is very long fibred (60–110 mm), one is of intermediate fibre length (10.5–24 mm), and one is short fibred (7–14 mm). The ulnar head shows fibre lengths ranging from 12 to 38 mm and the radial head consists of fibres of 5.5–8 mm. The physiological cross-sectional area was 288 cm² for the superficial and 317 cm² for the deep digital flexor muscle, respectively.

This study presents data on the heterogeneous architecture of equine digital flexor muscles. How it relates to their passive elastic properties and function needs to be investigated further.

We would like to thank the Horserace Betting Levy Board for their support.

¹Wilson A.M., et al. (2001) *Nature* 414: 895–899.

²Hermanson J.W., Cobb M.A. (1992) *J. Morphol.* 212: 269–280.

A9.23—Mechanical properties of the hoof horn of the sole of dairy cows and its relationship to haemorrhage level and lameness

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The structural strength of the hoof sole tissue was studied in 36 dairy cows calving in the autumn of 2000. Samples of hoof sole tissue of 0.1–0.3-mm thickness were collected from all claws at 40, 100 and 160 days post-partum. At the same time, the cows had their feet scored for lesions. Sole and white line areas of each claw were analysed for puncture resistance and elastic modulus on a TA.XT2i texture analyser (Stable Micro Systems). Samples were scored for level of haemorrhage, using a scale of 0–5. The thickness of the tested area was recorded simultaneously. The data were analysed by ANOVA–GLM, using cow, claw and collection period as fixed parameters and thickness as a covariant.

The force required to puncture the samples was significantly ($P < 0.01$) lower in samples with high haemorrhage scores (8.72, 8.53, 8.06, 7.75, 6.08 and 4.99 N for scores 0–5, respectively). The puncture resistance and elastic modulus of the sole horn was significantly greater ($P < 0.01$) in the front claws (8.84 N and 92.8 N/mm²) that had lower lesion scores, when compared to the hind claws (7.94 N and 86.8 N/mm²), and decreased when the lactation progressed and the scores for lesion and lameness increased ($P < 0.001$). The puncture resistance of the white line did not differ significantly between claws but was significantly lower at day 160 ($P < 0.001$). The puncture resistance of the sole horn was significantly greater than the puncture resistance of the white line horn ($P < 0.01$) (8.41 vs. 5.62 N).

A9.24—Quadrupedal and bipedal walking in bonobos: dynamic plantar pressure distributions

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In this study, we analyse plantar pressure distributions of the quadrupedal and bipedal locomotion of the bonobo ('pygmy chimpanzee'), *Pan paniscus*, collected during terrestrial walking of seven individuals ($N = 90$). Therefore, we used a 7-m-long catwalk with three built-in force plates and Footscan pressure mats (RSscan).

Functional foot length, degree of hallux abduction and total contact time were determined on the Footscan images, and plots, showing pressure as a function of time, for six different foot regions, were generated. We also studied five adult humans for comparison ($N=13$). Both gait types of the bonobo show a large variation in plantar pressure distributions, which can be due to the interference of behavioural factors with locomotion. The heel and the lateral midfoot typically touch down simultaneously at initial ground contact in bipedal and quadrupedal walking of bonobos, in contrast with the typical heel-strike of human bipedalism. We observed a varus position of the foot and a mid-tarsal break in both locomotion types. The course of the center of pressure shows a pronounced latero-medial shift near the metatarsal heads during quadrupedalism, as a consequence of the medial weight transfer during mid-stance. Bipedal locomotion of bonobos is characterised by a more plantar foot posture and by a shorter contact time than during quadrupedal walking, according to a smaller stride and step length at a higher frequency. These quantitative differences between quadrupedalism and bipedalism are subtle, and both gait types can not clearly be separated on the basis of plantar pressures alone.

A9.25—Walking in bonobos: no evidence for an inverted pendulum mechanism

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There is considerable debate whether bipedal early hominids had an efficient, straight legged, gait or a (probably less efficient) 'bent-hip, bent-knee' gait. We analysed center of mass (COM) fluctuations in bonobos (*Pan paniscus*), most likely the best extant 'model' for early hominids, to verify whether an efficient inverted pendulum mechanism, as found in humans, is present. Because bonobos are quadrupedal as well as facultative bipedal walkers, both locomotion types are compared.

In humans, the COM movements during walking have been studied profoundly. A double humped vertical ground reaction force (GRF), reflecting the acceleration of the body's COM, characterizes human walking. Kinetic and potential energy of the COM are in anti-phase, which allows for an external energy exchange system, often referred to as the 'inverted pendulum mechanism'.

With this in mind, we analysed COM fluctuations of bipedal and quadrupedal terrestrial locomotion in bonobos. Morphometric, kinematic and GRF data were obtained using an integrated set up in a zoo environment. The registered vertical GRF data show single humped curves in both bipedal and quadrupedal locomotion. In both locomotion types, no inverted pendulum

was thus found. Moreover, no stereotyped phase relationship between kinetic and potential energy could be observed at all. We conclude that COM fluctuations in bonobos differ considerably from those observed in humans and that, most likely, walking efficiency is smaller. Possible ultimate explanations may be that the bonobo locomotor apparatus is tailored for other locomotion types, e.g. climbing, or that terrestrial efficiency is of less importance.

A9.26—Oscillations of the body's centre of mass in new walkers

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In biomechanics, whole body movements are often characterised by movements of the body's centre of mass (BCM). This pilot study on development of walking in infants focusses on these BCM movements. An able-bodied infant was videotaped (50 Hz) every 2 weeks from the onset of independent walking until 6 weeks thereafter. Frontal and lateral views were digitised (18 body points: head, joint centres and feet) and analysed with APAS, resulting in segmental and joint kinematics. The position of segmental CM and mass distribution were determined on external morphometry (Crompton et al., 1996) allowing us to calculate, in three dimensions, the BCM. The three-dimensional oscillation of the BCM is complex, but can be divided into a lateral and vertical oscillation, both resembling a sinusoidal wave. The relative amplitude of the infants' lateral oscillation is large in comparison to adults (4.2% of total body length vs. 3.3%), showing a rapid decrease with increasing walking experience. Balance problems might account for this observation. Prolonged double support phase and immature coordination point towards a lack of balance in new walkers. An increase in stability is gained by walking with a wide support base. Possibly, infants who have immature coordination tend to keep their BCM almost over the supporting limb to minimize the chance of falling.

Crompton et al. (1996) *Am. J. Phys. Anthropol.* 99: 547–570

A9.27—Prey capture kinematics of clariid catfishes

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Some species of airbreathing catfish of the family Clariidae have extremely well developed (hypertrophied) jaw closing muscles. Consequently, these catfishes are particularly suitable to investigate the effects of a morphological specialisation (jaw adductor hypertrophy) in

a complex integrated system (cranial musculo–skeletal apparatus of fish). The effects of such enlarged jaw muscles on feeding mechanics are, apart from a (theoretical) higher maximal biting force, still unknown. Compared to *Clarias gariepinus*, which has relative small jaw closers, *Clariallabes* sp. shows a clear hypertrophy of the jaw adductors. High-speed video recordings and X-ray film recordings were made of these two species feeding on two different prey (shrimp and a piece of cod). Contradictory to the expectations of earlier morphological research, these experiments reveal that suction feeding (and not only biting) is of great importance to the tested catfishes. An extensive strike-to-strike variability was observed. On the other hand, no obvious effects of prey type were found. Yet, both species modulate the magnitude of neurocranial elevation in function of the prey position. Some differences in cranial movements between the two species during prey capture, such as faster mouth closing and reduced lateral expansions of the skull, are possible consequences of the more developed jaw adductors. Further research including species with more extreme jaw closer hypertrophy, such as *Channallabes apus*, is in progress.

A9.28–Mechanical properties of the passive component of force enhancement

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We discovered that the steady-state component of force enhancement following active muscle stretch is associated with a passive component. Here, we characterized the mechanical properties of this passive component with the goal to determine its possible origin. Testing was done in 10 cat soleus muscles. We found that the passive component of force enhancement was long lasting (more than 30 s), but could be abolished instantaneously by shortening of the muscle to its initial length. The passive force enhancement decreased at a greater rate and was stiffer than the corresponding passive force following isometric reference contractions. It decreased in a dose-dependent manner, with the amount of shortening preceding active muscle stretch. We conclude from these results that the passive component of force enhancement must lie in parallel with the contractile components, has visco-elastic properties, and can change its elasticity instantaneously upon shortening a sufficient amount. Furthermore, it allows force enhancement to exceed the peak isometric force at optimal muscle length, thereby disqualifying any mechanism based on sarcomere length non-uniformity as an exclusive and viable explanation for the steady-state force enhancement following active muscle stretch. We propose that titin could be the structural component responsible for the passive force enhancement by actively changing its stiffness when muscle is stretched great amounts at long muscle lengths. Such a change in stiffness could be asso-

ciated with an increased strength of the molecular bonds in the immunoglobulin domain or by a change in the attachment site of titin to myosin upon contraction.

A9.29–How frogs jump out of water

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Euphlyctis cyanophlyctis and *Euphlyctis hexadactylus* are two common species in Sri Lanka, and in the rest of south Asia. Both species are known for their habit of skipping over the water surface. The frogs start from a floating position, and then bounce five or six times before diving to the bottom. Equally remarkable is their ability to leap from this floating position up to 50 cm in height to catch an insect flying by. We studied these unique abilities by videotaping both species in these different behaviors. In this poster, we focus on their leaping abilities. We were able to videotape 119 sequences ($E \cdot h = 70$; $E \cdot c = 49$) by holding a dragonfly approximately 30 cm above the water surface. This triggered the leaping behavior. We used a JVC camcorder at 100 Hz. We examined the mechanism behind this extraordinary performance by measuring the hind leg movements.

The leaping behavior is realized by fast extension of the hind legs (up to an extension time of merely 0.03 s) and by holding the maximal distension of the webbing as long as possible. When the legs approach the free water surface, webbing is closed quickly to minimize the contact surface.

A9.30–Muscle activation, length change and power output of the m. hyohyoideus of the carp

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We investigated the function of the m. hyohyoideus superior (MHS) and inferior (MHI) in the head of carp (*Cyprinus carpio* L., 29.7 ± 2.1 cm fork length, $N=3$) during three movements (breathing, stressed movements and food uptake). Two hypotheses were investigated: (1) the MHS is mainly active during fast movements, whereas the MHI mainly restricts its activity to slow sustained movements; and (2) the MHS and MHI of carp act as agonists instead of antagonists, as mentioned earlier in literature for, e.g. the perch (*Perca fluviatilis* L.) and the ruff (*Gymnocephalus cernua* L.)^{1,2}. We measured both the muscle activities and strain patterns of the MHS and MHI using electromyography and sonomicrometry, respectively. We also recorded head movements from a ventral viewpoint (high-speed video, 250 frames s^{-1}). From breathing to stressed movements to food uptake, an increase was found in muscle strain

range, cycle frequency and (relative) stimulus duration while stimulus on- and offset occurred earlier in the strain cycle. Also, the MHS and MHI were always active simultaneously. These findings indicate that: (1) the MHI cannot be responsible for high frequency movements (i.e. stressed movements and food uptake); (2) the m. hyohyoideus assists in the onset of opercular closing; and (3) the MHS and MHI act as agonists.

¹Osse, J.W.M. (1969) *Neth. J. Zool.* 19; 289–392.

²Elshout-Oldenhove M.J.W., Osse, J.W.M. (1976) *J. Morph.* 150; 399–422.

A9.31—How strong are red muscle fibres from the dogfish *Scyliorhinus Canicula*?

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We have re-examined the isometric stress (force/cross-sectional area) produced by bundles of red muscle fibres

isolated from dogfish. These fibres are small in diameter and held together tightly by connective tissue; some fibres are likely to be damaged and become non-contractile during dissection of the fibre bundles. We report here experiments on red muscle in which fibres have been stained to distinguish intact from damaged fibres. In bundles of red fibres, $68.6 \pm 1.8\%$ (mean \pm S.E.M., $N=19$) of the total fibre cross-sectional area ($0.843 \pm 0.055 \text{ mm}^2$) consisted of intact fibres. The isometric stress produced by red fibre bundles from which damaged fibres had been removed was $142.4 \pm 10.3 \text{ kN m}^{-2}$ (mean \pm S.E.M., $N=35$). In white fibre bundles damaged and intact fibres can be distinguished after fixing in alcohol without any staining. The isometric stress produced by white fibre bundles from which damaged fibres had been removed was $289.2 \pm 8.4 \text{ kN m}^{-2}$ (mean \pm S.E.M., $N=25$). Thus red fibre bundles produce less force per cross-sectional area of intact fibres than white fibre bundles. Part, but not all, of the difference can be explained by the larger area occupied by mitochondria in red than white fibres (Bone et al., 1986).