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A11–GENERAL BIOMECHANICS

Organised by P. Aerts and J.L. Van Leeuwen for the Biomechanics Group

A11.1

Physiological and morphological basis of individual variation in jumping performance of *Hyla multilineata*

R.S. James, (Biosciences, Coventry); R.S. Wilson, (Zoology, Queensland); J.E. de Carvalho, T. Kohlsdorf, F.R. Gomes and C.A. Navas, (Biosciences, São Paulo)

Frog jumping is an excellent model system for examining the structural basis of interindividual variation in burst locomotor performance. When standard projectile equations have been applied to jumping they predict performance should be improved by increased hindlimb length, increased mass of jumping muscles and alteration of the origin and/or insertion of jumping muscles (for review see Emerson, 1995). We used the tree frog *Hyla multilineata* to examine the range of morpho-physiological traits that underlie interindividual variation in jump performance. Maximum jump distance and several possible factors that affect jump performance, such as body size, hind limb length, muscle mass, muscle mechanical and biochemical properties were analysed for 38 individual frogs. We found maximal jump distance was significantly repeatable ($P < 0.001$) within individuals. When body length or body mass effects were removed, around 50% of the interindividual variation in jump distance was explained by the combined variation in pyruvate kinase activity of the hindlimb muscles and plantaris mass.

Emerson, S.B. (1985). In *Functional Vertebrate Morphology* (ed. M.E. Hildebrand et al.), pp. 58–72. Cambridge: Harvard University Press.

A11.2

Wet adhesion in tree frogs

W.J.P. Barnes, M.O. Riehle and J.M. Smith, (IBLS, Glasgow); W. Federle, (Zoology II, Würzburg)

On both theoretical and experimental grounds there is a need to reassess the traditional view that tree frogs adhere almost exclusively using the capillarity forces of wet adhesion. The use of both fluorescence and inter-

ference reflection microscopy on living, adhering tree frogs (*Litoria caerulea* and *Hyla chrysocelis*) indicate that tree frogs adhere much more closely to their substrates than had been suspected, the thickness of the fluid layer between pad and substrate having values as low as 50nm at the flat surface of the toe pad epithelial cells. This, together with evidence for high coefficients of friction between toe pads and surfaces like glass and Perspex, indicates that, for angles of up to 90°, frictional forces will play an important role in tree frogs climbing on smooth surfaces. Also, even though the mucus produced by the toe pad mucous glands has a low viscosity, the small pad/substrate distance means that we cannot rule out a significant contribution from the viscosity forces (Stefan adhesion) of wet adhesion over the whole range of angles at which tree frogs can adhere (up to 180° in some species). Indeed, there are theoretical reasons why it is not as easy to separate the contributions of viscosity and surface tension to wet adhesion by their scaling factors as has been thought hitherto. It is clear that we still have much to learn about wet adhesion in tree frogs.

A11.3

Abstract not supplied

A11.4

Myotomal anatomy in zebrafish: Mapping three-dimensional white muscle fiber angles using cross-correlation image analysis

E.D. Tytell, (Organismic and Evolutionary Biology, Harvard University)

Cross-correlation based image analysis techniques, such as particle image velocimetry (PIV), have been used successfully to track particles moving in fluids. While

these techniques are normally applied to a series of particle images over time, they can in principle track any texture through a series of images taken over time or space. This study applied a modified PIV algorithm to serial sections of white muscle in zebrafish, *Brachydanio rerio*, to determine the 3D fiber angles. Thick sections of whole adult zebrafish were taken in the transverse and horizontal planes and optically sectioned using confocal microscopy. Three-dimensional vector fields showing the fiber orientations were then produced at each plane throughout the body. The surfaces of the myosepta in 3D were also reconstructed by manual digitization from the serial sections. Previous studies have constructed “muscle fiber trajectories” by following a muscle fibers through many myomeres, assuming that separate muscle fibers follow an overall trajectory through the myomeres. This assumption will be evaluated by comparing the orientation of muscle fibers inserting on a myoseptum to the angle of those originating from the same myoseptum. Finally, muscle fiber trajectories from many points in the body will be calculated and compared to these previous results.

A11.5

Differential recruitment of motor units during locomotion

J.M. Wakeling, (Royal Veterinary College, London)

Muscles are used for a variety of different tasks during a locomotor stride, including weight support, limb positioning, energy storage and providing the power for propulsion. During routine movements the muscles are typically used at submaximal levels so that not all motor units are used at any given time. It is therefore possible that an animal will select different motor units for the different movement tasks within a stride. The purpose of this study was to test the hypothesis that motor units within mammalian muscle are differentially recruited for different movement tasks. Six runners completed a randomized protocol of walking and running at three different speeds. Myoelectric signals were recorded from nine lower extremity muscles using surface electrodes; resolved into their spectra at different time periods within each stride using wavelets; and compared using principle component analysis. The principle components provided a measure of the frequency content of the myoelectric spectra. Distinct frequency patterns were observed between the spectra and could be distinguished between different periods within each stride and between different muscles. These spectral patterns matched those previously identified for activity from the different types of motor unit within the lower extremity muscles. It is suggested that the different motor units within a lower extremity muscle are differentially recruited for different movement tasks during locomotion, and that this is a common occurrence even at moderate locomotor speeds.

A11.6

Preferential recruitment of motor units during locomotion

A.I. Rozitis, (Human Performance Laboratory, University of Calgary, Canada); J.M. Wakeling, (Structure and Motion Laboratory, Royal Veterinary College, UK)

Myoelectric signal from mixed mammalian muscle may be used to determine motor unit recruitment patterns since different types of motor units generate different frequency spectra within a myoelectric spectrum (4). It has been suggested that the faster muscle fibres are preferentially recruited to power faster movement tasks, such as fast starts and fast swimming in fish (1, 2) and during the cat paw shake (3). This makes mechanical and energetic sense as the slower muscle fibres would contribute little, if any, to the power output of the muscle. Recruitment patterns of muscle fibres within a muscle during locomotion have not been investigated. The aim of this study was to test the hypothesis that higher frequencies appear in the myoelectric spectra during faster activities. Trained cyclists completed a series of trials across a range of cadences (50–140 rpm) and torque (100–500 Nm) combinations. EMG was measured on nine muscles of the lower extremity, using round, bipolar surface electrodes. Using wavelet and principle component analysis, increased high frequency with decreased low frequency myoelectric activity was observed in the cycling conditions which required faster muscle fibre shortening and low muscle force. These observations suggest that differential recruitment is a good strategy for motor unit recruitment within a muscle.

1. Jayne and Lauder (1994) J. Comp. Physiol. A 175: 123–131.
2. Rome et al. (1988) Nature 333: 824–827.
3. Smith et al. (1980) J. Neurophysiol. 43: 612–620.
4. Wakeling et al. (2002) J. Exp. Biol. 205: 359–369.

A11.7

Direct measurement of plantaris longus muscle power in the frog *Rana pipiens*

D.R. Peterson, M. Kaya and W. Herzog, (Human Performance Laboratory, University of Calgary)

Frog muscles have been said to have contractile properties that far exceed those observed in humans, so much so that the leaping ability of many frogs must be considered impossible, or at least incomprehensible (Lutz and Rome, 1994). Thus, frog muscle power has been studied extensively. However, power has been calculated only theoretically, as direct muscle force measurements in this system are difficult to do. Here, we measured the power output of frog plantaris longus (PL) by direct tendon force measurement (buckle), direct fibre length

recording (sonomicrometry), and muscle-tendon unit length determination (tendon travel). Power was calculated as the product of tendon force and rate of change in muscle length and as a tendon force and rate of change in fibre length. The former gives the correct instantaneous power of the muscle tendon unit, the latter is not a proper measure of power, but one that has been used in the literature (e.g. Roberts et al., 1997), and thus served for comparison purposes. The average peak power produced by the entire PL muscle-tendon unit was 712 ± 47 W/kg; the “power for PL fibres” was 118 ± 10 W/kg. While the fibres shortened slowly throughout the movement, the entire muscle did not shorten initially, but shortened at a much greater rate than the fibres later in the movement. Thus, the action of the elastic elements uncouples the shortening velocity of the entire muscle-tendon unit compared to the fibres, and allows for peak power production that could not be achieved by the contractile components alone.

A11.8

In vivo segment length changes in relation to in vitro force-length properties in the toad semimembranosus muscle

A.N. Ahn and A.A. Biewener, (Organismic and Evolutionary Biology, Harvard University)

There is evidence that adjacent muscle segments can contract heterogeneously under in vivo conditions implying that the two segments (and their sarcomeres) may operate on different regions of their force-length relationships simultaneously. To examine this issue, we measured central and distal segment strain patterns in vivo using 3 sonomicrometry crystals implanted along the length of the semimembranosus muscle in the American Toad (*Bufo americanus*; $n=7$) to record adjacent segment strains in vivo during hopping. On the same day, we compared the lengths measured in vivo to their respective in vitro force-length properties at various stimulation levels (tetanic, 200 Hz for 50 ms; 200 Hz for 25 ms, and twitch). In vivo during hopping, the central muscle segment operated on the plateau region of its force-length relationship, beginning at a relatively longer sarcomere length and only shortening during hopping. Simultaneously, the distal segment operated on the ascending limb of its force-length relationship. The ascending region provided stability for the sarcomeres in the distal region, which stretched then shortened during hopping. Two adjacent segments can operate on different regions of their force-length relationships simultaneously both in vivo and in vitro. Understanding regional differences within muscles in vivo will allow us to link our understanding of sarcomere behavior with whole muscle behavior during locomotion.

A11.9

Transient force growth following depression in whole skeletal muscle

D.T. Corr and W. Herzog, (Human Performance Laboratory, Canada)

The depression of isometric force following active shortening is a well-accepted characteristic of skeletal muscle, yet its mechanism remains unknown. While traditionally analyzed at steady-state, transient phenomena caused, at least in part, by cross-bridge kinetics, may provide novel insight into the mechanism associated with force depression (FD). Therefore, we investigated the transient forces following active shortening to possibly gain additional insight into the cause of FD. FD following active shortening was determined in cat soleus ($N=8$), in situ, using experimental methods previously described [Herzog and Leonard (1997) *J. Biomech.*]. In these experiments shortening amplitude and shortening speed were systematically varied. The transient force following active shortening, $F(t)$, (muscle held at final length while tetanically stimulated), was fit ($R^2 > 0.99$) using an exponential function, $F(t) = F_{\text{inf}} - Ae^{-kt}$ where F_{inf} represents the depressed force at steady-state, A the recoverable force, and k the exponential growth rate. A complete-block ANOVA indicated that k decreased with shortening amplitude and increased with speed, with no amplitude-speed interaction, and that steady-state FD increased with shortening amplitude. Regression analyses showed that muscle mechanical work correlated positively with steady-state FD and shortening amplitude, and negatively with k and shortening speed. Thus, an increase in shortening amplitude, or an increase in muscle mechanical work, would decrease growth rate and increase steady-state FD. These results support a proposed mechanism where FD is caused by a reduction in cross-bridge attachment rate (slower force growth) in the newly-formed zone of actin-myosin overlap (larger with increased shortening) [Maréchal and Plaghki (1979) *J. Gen. Physiol.*].

A11.10

Muscle tendon unit interaction during controlled dynamic contractions

G.A. Lichtwark, (University College London); R. Weller and A.M. Wilson, (Royal Veterinary College)

The timing of muscle shortening during locomotion is key in achieving optimum muscle function. Determining how muscle fibres and their attached tendons interact during movement is however difficult. When a muscle contracts in vivo several things happen that we can measure; the tendon and aponeurosis lengthen, the muscle fibres change length and often orientation and the

entire muscle changes shape. Here we used a combination of measurement techniques to examine these changes in the *triceps surae* muscle group during a range of dynamic activities. Motion analysis was used to measure the cross-sectional area changes of the muscle group at different levels during isokinetic and isometric plantar flexion. Motion analysis was also used to track the motion of anatomical landmarks and of an ultrasound probe. Simultaneous ultrasonic imaging was used to determine muscle fibre lengths, muscle fibre orientations and the position of muscle tendon junction. Finally force measurements were made with a isokinetic dynamometer and muscle activity was measured with EMG. Similar techniques were then applied during walking and running. Combining these techniques has allowed us to determine how the contractile and series elastic components of the muscle tendon unit interact to produce force and work during dynamic movements and running. Significant storage and return of elastic energy within the Achilles tendon and aponeurosis was found to occur during running but the muscle fibres were almost isometric when the tendon force was high. This analysis gives us a greater understanding of how muscles operate to optimise performance.

A11.11

Running in a rough environment: the mechanical influence of limb posture and ankle extensor dynamics on stability in running guinea fowl

M.A. Daley, (Organismic and Evolutionary Biology, Cambridge)

How do animals maintain stability in the face of unexpected disturbances during locomotion? This study investigates how limb and muscle dynamics respond to sudden changes in substrate level during avian bipedal running. Guinea fowl ran along a runway that contained an 8 cm drop in substrate height in the middle. During 'surprise step' trials, the drop was camouflaged using a 'false floor' made of paper, while in 'visible step' trials the bird was allowed to see the upcoming drop. Ground force and high-speed video recordings were taken simultaneously with in vivo measures of muscle force, length and activity from the lateral gastrocnemius (LG) and digital flexor-IV (DF-IV). In surprise step trials, limb and muscle dynamics do not initially differ from level runs. However, shortly after contact, the limb breaks through and continues to extend until the substrate is again encountered. The subsequent limb and muscle dynamics depend on the speed of movement. During visible step trials the bird adjusts limb and muscle dynamics before the first step down. Of the two muscles studied, the DF-IV shows greater changes in muscle dynamics associated with changes in limb posture. In

both surprise and visible step trials, much of the COM recovery from the perturbation occurs over more than one step after the initial step down. (Supported by an HHMI Predoctoral Fellowship and NIH R01-AR047679 to A.A.B.)

A11.12

The role of Triceps brachii in equine locomotion

J.C. Watson, A.M. Wilson, (Structure and Motion Lab, Royal Veterinary College)

Triceps is the largest forelimb muscle in the horse (mean 4.5kg, $n = 13$). It is composed of three long fibred muscle heads each capable of considerable length change (fascicle lengths range from 12 to 24cm). Triceps is an elbow extensor and shoulder flexor and is usually regarded as functioning to counteract gravitational and inertial forces during stance. The muscle architecture however suggests a more dynamic role involving power generation or absorption. We hypothesise that triceps is not an antigravity muscle but instead functions to decelerate the limb and initiate retraction at the end of the swing phase. We collected surface EMG from the long and lateral heads of triceps in six horses during treadmill locomotion at walk, trot and canter. We then repeated the experiment with a 0.75kg mass attached to both digits. Wavelet decomposition of the EMG signal was used to resolve muscle activity into six frequency ranges. The wavelets were then integrated to give an estimate of muscle work. Preliminary data collected at trot shows that triceps is active in late swing and early stance phase but not during the rest of stance. Other muscles must therefore act as elbow extensors in stance. There was significantly more activity in the lateral head ($p = 0.04$) when weights were attached to the legs. These data support our hypothesis that triceps generated more force to decelerate a heavier limb. Triceps can also co-contract against biceps to stiffen the limb prior to contact.

A11.13

Mechanical power output in leaping rock wallabies

C.P. McGowan, (Harvard University); R.V. Baudinette, (Adelaide University); A.A. Biewener, (Harvard University)

Much of what we know about animal locomotion has come from studies of animals moving at steady speeds over level surfaces. Yet in the wild animals are faced with highly variable environments in which they must maneuver. It is likely that these non-steady activities place the greatest demands on the musculoskeletal system of animals. The goal of this study was to examine how

yellow-foot rock wallabies (*Petrogale xanthopus*), a species that inhabits steep rocky cliffs, produce and modulate mechanical power in steep jumping maneuvers. In the wild, these animals have been reported to make jumps to well over five times their hip height. In this experiment, five adult wallabies were hopped in an outdoor runway containing a stepped ledge 110 cm high (over three times hip height). High-speed video (250Hz) was recorded from the lateral aspect and synchronized with the ground reaction forces measured via a forceplate mounted in the runway at the point of take off. Analysis of center of mass mechanics revealed that the mean mechanical power produced during the stance phase of these jumps was quite high, averaging 678 W/kg leg muscle. A more detailed inverse dynamics analysis will be used to determine individual joint power and timing, and thus better understand the mechanisms by which these animals produce such high mechanical powers. Comparable powers have been recorded in standing jumps from frogs and bush babies, but the moving jumps in our study likely require the wallabies to employ different mechanisms than those proposed in previous work.

A11.14

Proximal hindlimb muscle strain and activation patterns in goats: Do differences in animal size impact limb muscle function?

G. Gillis, (Biological Sciences, Mt. Holyoke College); A. Biewener, (Organismic and Evolutionary Biology, Harvard University, USA)

Mammals that differ greatly in size generally adopt distinct limb postures during locomotion: small animals typically remain more crouched relative to large animals. It is now widely accepted that the more upright posture of large mammals serves to align limb bones more vertically, reducing ground reaction moments at their limb joints. However, despite our understanding of this scaling of limb configuration, we know little about how such postural differences influence the in vivo strain of limb muscles. In this study, we used sonomicrometry and electromyography to explore fascicle length change and activation in two major hindlimb extensors of the goat, the biceps femoris (hip extensor) and vastus lateralis (knee extensor). We then compared our results from goats (15–25kg) to data from rats (225–260g) to discern if limb muscle strain regimes were comparable across such divergent taxa. In both species, the biceps shortens substantially during stance (20–30% of resting length, L_0) and is active over much of this interval. The vastus undergoes a stretch-shorten cycle during stance in both species, however, the degree of stretching vs. shortening differs markedly. In goats, vastus fascicles stretch relatively little over the 1st half of stance (6–9%

L_0) but then shorten twice as much over the rest of stance; the reverse is true in rats where fascicles initially stretch much more than they subsequently shorten. Future studies will explore more closely related species and ontogenetic series to clarify better the role that body size and limb posture play in mediating limb muscle strain during locomotion.

A11.15

How fish larvae swim: lessons from flow fields and kinematics

U.K. Müller, J.G.M. van den Boogaart and J.L. van Leeuwen, (Experimental Zoology, Wageningen University, The Netherlands)

The small size of fish larvae has important consequences for their swimming kinematics and hydrodynamics. The positive correlation between tail beat frequency and body-length-specific swimming speed means that, in order to out-swim their much bigger predators, fish larvae must execute their tail beats very swiftly. We observed tail beat frequencies of up to 100 Hz during cyclic swimming. The muscles powering this behaviour have very short contraction cycles of 10 micro seconds, comparable to the fastest cyclic vertebrate muscles. The concurrent high body curvature induces considerable muscle strains of up to 0.06 in the white muscles and up to 0.19 in the superficial red muscles. The low swimming speed and body size of fish larvae also puts them in an intermediate flow regime, exposing them to significant inertial as well as viscous fluid forces. To understand the mechanisms that power swimming during the first 14 days of larval development, we explored the kinematics and flow patterns of three behaviours: cyclic swimming, slow bursts and startle responses. The flow patterns of cyclic swimming resemble the vortex arrangements of larger undulatory swimmers. Differences from larger fish become most apparent in the flow generated by coasting larvae, which entrain a rapidly growing body of water. Larvae are enveloped by a growing layer of high-shear and high-vorticity flow, and gradually an additional layer of reversed vorticity develops inside the original boundary layer (cf. van Leeuwen et al., A11.16).

A11.16

Why fish larvae change gait during development

J.L. van Leeuwen, U.K. Müller and J.G.M. van den Boogaart, (Experimental Zoology, Wageningen, The Netherlands)

Fish larvae switch swimming styles as they grow: as hatchlings, they swim predominantly in a cyclic manner,

5 days post-hatching, they burst-and-coast. One of the constraints governing this switch might be hydrodynamic: larval body shape changes drastically during yolk sac absorption. While the yolk sac is relatively large, drag might make coasting unfeasible, forcing cyclical swimming. To investigate the role of the changing drag in the switch from cyclic to intermittent swimming, we recorded larval swimming and coasting performance as well as the flow patterns (2D PIV) generated by coasting larvae ranging from 0 to 5 days after hatching. Coasting distance correlates only weakly with age, lending only weak support to our drag hypothesis. Coasting performance is confounded by the larva's gradually improving trim: hatchlings nosedive towards the end of the coast because they have immature pectoral fins and no swim-bladder; once both are fully developed, the larva is able to maintain a horizontal orientation. The flow patterns around coasting fish larvae look very similar for the studied age range. The larva entrains a rapidly growing body of water. The areas of high shear and high vorticity in this boundary layer move away from the larva over the duration of the coasting phase, and a new area of elevated vorticity develops near the fish. We quantified the influence of the body shape and boundary layer development on the coasting performance using 2D and 3D computational fluid dynamic models which agreed well with our experimental observations.

A11.17

Hoop jumping in frogs: Estimating the propulsive thrust of swimming frogs using a vortex ring approach

E.J. Stamhuis, (University of Groningen, The Netherlands); S. Nauwelaerts and P. Aerts, (University of Antwerp, Belgium)

When actively swimming, frogs produce thrust mainly by kicking their feet backwards. During the kicking motion, the webbed feet are spread and water is accelerated backwards, making the frog's body move forward. At the end of the stroke, the frog pulls its feet out of the accelerated masses of water, leaving behind a vortical wake. We studied the wake of frogs swimming through laser illuminated planes in a particle seeded aquarium. Recorded images were analysed using DPIV (Digital Particle Image Velocimetry). The results demonstrate that the frogs produce two clear vortex rings during each kick. These vortex rings do not interact during their generation phase, neither during the first part of their free life. This leads us to the conclusion that the previously postulated thrust-enhancing mechanisms, such as reflective or wedge action, do not exist. Furthermore, the vortex rings showed all the characteristics necessary for the application of a vortex ring model to calculate the momentum in the rings. The average thrust

forces generated during the kicks were derived from the momentum calculations. Comparison with a parallel study on thrust mapping during the leg extension phase showed that mapping the characteristics of vortex rings resulting from frog swimming may yield a good estimate of the average propulsive force during the kick phase.

A11.18

Propulsive force calculations in swimming frogs using a momentum-impulse approach based on PIV flow information

S. Nauwelaerts, (Antwerp University, Belgium); E. Stamhuis, (Groningen University, The Netherlands); P. Aerts, (Antwerp University, Belgium)

Frogs are animals that are capable of locomotion in two physically different media, water and air. The comparison of kinematics of swimming frogs revealed a difference in propulsive impulse between jumping and swimming. To explore this difference further, we determined the instantaneous forces during propulsion in swimming using a impulse-momentum approach based on DPIV flow data. The obtained force profile was compared with force profiles obtained from drag-thrust equilibrium of the center of mass and with the force profiles generated during jumping. The impulse-momentum approach was based on the estimation of the change in volume and velocity of the water mass influenced by the kicking feet. This new approach to quantifying the instantaneous forces during swimming was tested and proved to be a valid method of determining the external forces on the feet of swimming frogs.

The application of the impulse-momentum approach on 8 swimming sequences exposed a slight overestimation of the drag coefficient in the drag-thrust calculations indicating that the difference in impulse between jumping and swimming in frogs is even larger than previously stated. The difference between the force profiles lies, apart from a slightly higher peak force during jumping, mainly in a difference in shape. During swimming, maximal force is reached early in the extension phase, after about 20%, while during jumping, peak force is attained at 80% of the extension phase. This difference is in turn caused by a difference in interlimb coordination.

A11.19

Simulation-based biofluid dynamics in animal locomotion

H. Liu, Y. Inada, and H. Wang, (Chiba Univ./PRESTO, Japan)

Biological mechanical phenomena in swimming and flying are, in general, of 'Complex Systems', although some mechanisms behind it may be quite simple if

unveiled, but it needs to be modeled as realistic as possible so that we could avoid some pitfalls. Conventional paradigm for understanding of power and energetics in swimming and flying relies exclusively on the consistent potential theories to analyze the physics qualitatively as well as the observations and measurements to visualize the flow so as to support the theories. Recently, a new paradigm of the simulation-based biological fluid dynamics, has been showing great potential to elucidate the physics and mechanisms in the complicated biological fluid phenomena, which, by means of computational modeling of biofluid dynamics through faithful reconstruction of morphology and representation of realistic kinematics of individual object. In this paper we give a detailed description of the simulation-based biological fluid dynamics as well as applications in animal locomotion, with a special focus on an undergoing project: development of a biology-inspired dynamic flight simulator. In this project we aim at establishing an integrated computational mechanical simulator for a freely flying insect, which is capable to mimic the free flights involving hovering, forward flight and quick-turn based on realistically modeling of geometry and kinematics and accurately modeling of dynamics. It is expected that the developed simulator would provide also novel theories and technical innovations for research and development in the Micro Air Vehicles (MAVs).

A11.20

Hydrodynamics of swimming frogs: hindlimb-generated vortex wake patterns

L. Christoffer Johansson, (Theoretical Ecology, Lund University); George Lauder, (MCZ-labs, Harvard University, USA)

To test different hypotheses regarding the hydrodynamic mechanisms of frog swimming we used digital particle image velocimetry (DPIV) to determine/quantify the flow structure of the vortex rings produced by the feet during propulsion. Previous studies of the kinematics of swimming frogs have suggested that interaction between the feet, resulting in a jet, as the feet come together at the end of synchronized kicks may augment force production. Our results show, however, that each foot produces its own distinct vortex ring, in both alternating and synchronized kicking of the feet. There is no evidence of a jet being produced even during powerful synchronized kicks (maximum thrust calculated was 0.97 N per foot). The magnitude of the thrust (T) produced by the feet differs between alternate ($T=0.13 \pm 0.021$ N/foot) and synchronized kicking ($T=0.24 \pm 0.040$ N/foot), as do maximum swimming velocity, with higher swimming velocity and forces produced during the synchronized kicks. The kinematics of our surface swimming frogs (*Rana pipiens*) show that the frogs follow a

similar acceleration pattern as those in previous studies. The observed acceleration is thus not explained by a single jet produced by the merging feet at the end of the power stroke and alternative explanations are discussed.

A11.21

Dorsal and anal fin functional interaction in basal and derived teleostean fishes

E.M. Standen and G.V. Lauder, (Organismic and Evolutionary Biology, Harvard University, USA)

The dorsal and anal fins of fishes are median fins that function in concert with the tail during propulsion and maneuvering. But dorsal and anal fin kinematics are poorly understood, and no data are available on coordination patterns between these two fins and the tail over a range of swimming speeds and during maneuvering. In order to clarify patterns of median fin function in a diversity of teleost fishes, we filmed simultaneously with three high speed (500 fps), high resolution cameras (one at 1024×1024 , two at 1024×1280) to examine the interaction of the dorsal, anal and caudal fins in basal and derived teleosts (trout: *Oncorhynchus mykiss*, perch: *Perca flavescens*, sunfish: *Lepomis macrochirus*). In all species the height from the top of the dorsal fin to the bottom of the anal fin decreased as steady swimming velocity increased. Dorsal and anal fin undulation differed among species and depended upon steady swimming velocity. Of particular interest was the movement of the dorsal and anal fins during steady swimming in sunfish where fins began to undulate at 1.5 BL/s, showed maximal movement at 2 BL/s and reduced undulation at 2.5 BL/s. During maneuvering, all species showed a similar pattern where dorsal and anal fins appear to move together but opposite to the direction of the caudal fin. This interaction among median fins appears to aid in both thrust and stability during fish locomotion.

A11.22

Force transmission in the vertebral column of juvenile sea bass (*Dicentrarchus labrax*)

S. Kranenbarg, J.L. van Leeuwen, (Experimental Zoology Group, Wageningen, The Netherlands)

Sea bass (*Dicentrarchus labrax*, L.) is one of the two main species in the Mediterranean marine aquaculture. Lordosis is a significant problem in the aquaculture of sea bass. The severe vertebral deformation reduces biological performance, welfare and acceptability by the consumers. The causes of lordosis (high rearing temperatures, high water currents, failure of swim bladder inflation) are correlated with excessive swimming demands on the larvae. We hypothesize a functional

relation between the axial loading pattern and development of lordosis. We performed a μ CT study to analyse the ontogeny of lordosis in sea bass larvae. Our results show the detailed bone architecture of lordotic and non-lordotic vertebrae. Bone volume of lordotic vertebrae is higher than that of non-lordotic vertebrae. The extra bone in the lordotic vertebrae is deposited in areas of high compression (concave side of the lordosis). Lordotic vertebrae also show more trabeculae parallel to the long axis of the vertebrae. This suggests that architecture of a lordotic vertebra is indeed adapted to withstand the increased axial loading. The next step in our study is to make a finite element model and quantitatively compare the transmission of forces in lordotic and non-lordotic vertebrae.

A11.23

Does beam theory provide a valid description of muscle deformations of a swimming fish?

I.L.Y. Spierts, J. 't Hoen, M.H.M. Niessen and J.L. van Leeuwen, (Experimental Zoology Group, Wageningen University, The Netherlands)

The bending of the body of a swimming fish is assumed to occur like a homogenous beam. Muscle fibre strains are estimated using a sequence of dorsal views of a swimming fish and the exact axial muscle fibre orientations. During sustained undulatory swimming most fish use laterally situated red muscle fibres that run parallel to the fish axis. Experimental data showed that these red fibres behave as being part of a simple homogenous beam. For white muscle fibres, located closer to the fish axis, it is not clear whether this beam theory for muscle deformations holds. Contraction of the anterior epaxial musculature does not always cause bending of the fish axis at the same longitudinal position. In carangiform swimmers anterior white muscles develop force through which the posterior part of the body bends. Local bending therefore does not need to correlate to local strains. We determined two-dimensional white muscle deformations during fast starts of common carp (*Cyprinus carpio* L.), using 6 sonomicrometrical crystals that were positioned in corners of a trapezoid in a horizontal plane just above the spinal column at 0.55 FL. Distances between all crystals were measured, and fish were filmed in dorsal view using High-Speed Video (500 frames \cdot s $^{-1}$). Muscle strains calculated using the beam theory were compared with measured strains. It appeared that in carangiform swimming fish white muscle tissue does not behave as being part of a simple homogenous beam but show shear deformations that cannot be explained by the beam theory alone.

A11.24

The mechanics, sensory biology, and physiology of fish exploiting vortices

J.C. Liao, (Department of Organismic and Evolutionary Biology, Harvard University, USA)

Swimming fishes alter their pattern of body bending to exploit the energy of vortices shed behind a cylinder using a novel mode of locomotion termed the Kármán gait. However, the mechanism by which fish can sense these vortices remains unknown. To investigate, I blocked the lateral line system of rainbow trout (*Oncorhynchus mykiss*) using an established cobalt treatment. Vision cues were removed by conducting some experiments in complete darkness, where 850 nanometer infrared light emitting diodes and an infrared sensitive video camera allowed imaging of swimming motions. Tail-beat frequency, body wavelength, wave speed, and body amplitude were compared for fish Kármán gaiting under four treatments: with and without lateral lines in both light and dark experiments. Though fish under each treatment could Kármán gait, those without a lateral line introduce propulsive movements, had longer body wavelengths, and faster body speeds. For each treatment, head position was recorded every five seconds for one hour to determine location preference around the cylinder. Vision, even more than the lateral line sense, plays a crucial role in Kármán gaiting. In the dark, fish do not Kármán gait as often as when in the light. Instead, they take position to the side of the cylinder, illustrating another novel behavior that takes advantage of the energy present in the flow surrounding a cylinder. In the dark, fish with a lateral line will explore their flow environment, whereas without it they do not explore their environment to the same extent.

A11.25

Fishes out of water: the locomotor biomechanics of two amphibious blennies

S.T. Hsieh, (Dept. of Organismic & Evolutionary Biology, Harvard University, Cambridge, MA, USA)

The evolution of amphibious behaviour is surprisingly prevalent among fishes. Although blennies (Blenniidae) are characterized as being fully-aquatic and benthic in their habits, at least seven of 53 genera contain amphibious species. The Pacific leaping blenny, *Alticus arnoldorum*, have brought amphibious behavior in fishes to an extreme, and have even been described as being hydrophobic since they appear to actively avoid being submerged under water. They live in the high-energy surf zone and have evolved an extraordinary locomotor repertoire permitting rapid locomotion through complex, intertidal environments. These blennies regularly crawl

on horizontal surfaces, climb vertical, slippery surfaces, appear to skip across water, and can leap over four body lengths between rocks. All terrestrial motions appear stereotyped, involving a unique axial twisting motion of the tail. The crenulate-lipped rockskipper, *Praealticus labrovittatus*, also comes onto land, but much less frequently and does not exhibit axial tail twisting during terrestrial locomotion. Twelve individuals of *Alticus* and three individuals of *Praealticus* were filmed with two orthogonally-oriented high speed video cameras at 250 fps. Midline splines were obtained and transformed into three-dimensions using a custom program written in Matlab. Analysis of high-speed video suggests that tail twisting increases the overall efficacy of terrestrial locomotion of *Alticus*. Furthermore, the repetitive tail movements during these distinct locomotor modes suggest plasticity of tail function. Preliminary morphological investigation has yielded little difference between vertebral and caudal structure of *Alticus* and *Praealticus*. However, *Alticus* vertebrae do appear to be more loosely constructed, possibly allowing overall increased flexibility of the tail.

A11.26

Effect of gait on centre of mass movement

J.J. Robilliard, T. Pfau, T.H. Witte and A.M. Wilson,
(The Royal Veterinary College, London, UK)

Horses that pace out perform horses that trot in competition (the record time for harness race horses over a mile is 1 min 46 seconds at pace and 1 min 51 sec at trot). This has been suggested to be due to reduced external work as a result of decreased vertical oscillation of the centre of mass at pace. Here we compared competition horses that could perform both trotting and pacing gaits. Speed of locomotion was determined using a GPS data logger and movement of the COM predicted from a 6 degree of freedom inertial sensor mounted over the thoracic spinous processes. Horses exercised on a circular track pulling a jockey in a light-weight cart behind (as in competition). Data were double integrated with mean subtraction to calculate COM displacement. Angular displacement and angular velocity were calculated from gyroscope and inclinometer data. The potential energy change of the centre of mass through the stride was determined for each gait. The trunk was modelled as a cylinder and its angular momentum estimated. Angular velocity was then used to determine the energy associated with roll in each gait. Peak angular velocity occurred during the aerial phase when potential energy was also at a maximum. These two measures of COM energy are therefore in phase and can be summed. The data demonstrate that whilst pacers do have a reduced vertical oscillation of the COM, the extra energy associated with the greater roll results in similar external work in both gaits.

A11.27

Scaling of locomotor dynamics in horses

S.R. Bullimore and J.F. Burn, (Anatomy, Bristol, UK)

For mammalian species of different sizes to be able to move in the same way, systematic changes in limb anatomy with size must occur which compensate for the size-independence of tendon material properties (Bullimore and Burn, in press). Within mammalian species, adult individuals tend to occur in a relatively narrow range of sizes, so that such compensations are unnecessary. However, some domestic species have been bred to have a much wider size range. Because this has not arisen through natural selection, compensations for the effects of size may not be present. We tested the hypothesis that adult horses of different sizes do not move in the same way at equivalent speeds. The scaling of locomotion in geometrically similar horses with size-independent tendon properties was modelled theoretically. This indicated that the parameter most affected by size would be stride length relative to leg length (RSL). RSL was measured in 21 horses between 86 and 714 kg using optical motion capture. Data for a wide range of trotting speeds were obtained and interpolated to predict RSL at three equivalent speeds. At each of these speeds, RSL was not dependent upon body mass ($P > 0.50$), so the hypothesis was rejected. These results indicate that one or more factors must compensate for the effects of size in horses, allowing the same patterns of locomotion to be maintained over a more than 8-fold range of body mass. Future investigation will focus on identifying these factors.

A11.28

Inertial Sensors for Tracking Movements

T. Pfau, T.H. Witte, A.M. Wilson, (The Royal Veterinary College, London, UK)

Determining the vertical displacement of the centre of mass (CoM) is useful for estimating the external work of locomotion and in studying mechanics of locomotion. Whilst this can be achieved in the laboratory using optical motion analysis, such methods are difficult to apply during field locomotion. It is theoretically possible to determine displacement from double integration of acceleration but integration constants and changes in orientation present challenges in extracting meaningful data. Here we validate a small (40g) inertial orientation sensor comprising three linear accelerometers, three gyroscopes and three magnetometers for 6 degree of freedom (DOF) tracking. The inertial sensor was mounted on the withers of the horse using a harness and optical motion analysis was used to determine its 6 DOF position. The horse was then exercised on a treadmill at walk, trot and canter at speeds from 1.6 m/s to

11 m/s. Individual transducer signals were filtered and digitised within the sensor. Sensor orientation data were used to rotate the acceleration vectors into the horse reference frame. Linear displacements were then calculated by double integration of the accelerations. Data were mean subtracted before each integration to minimise integration errors (the CoM was assumed to follow a closed loop within a stride).

Means across speeds show root mean square errors between motion analysis and inertial sensor of below 15% of the range of movement for 3D-orientation and below 20% for 3D-displacements. The inertial sensor is therefore a useful tool for analysing CoM movements and is ideally suited for field experiments.

A11.29

Dissecting the Pogostick: Are all horse legs equivalent?

R. Weller, R.C. Payne and A.M. Wilson, (Royal Veterinary College, London, UK)

Leg stiffness scales with animal size and in the horse most of the length change occurs through load induced extension of the metacarpo-phalangeal joint (MCP). This extension is resisted by elongation of the deep and superficial digital flexor tendons (SDFT, DDFT) and the suspensory ligament (SL). We have previously shown that similar horses have similar leg stiffness but in a different study we showed that stiffness of the superficial digital flexor tendon (SDFT) varies by a factor of two between similar horse. We hypothesise that compliant tendons have a larger moment arm around the MCP joint to compensate for their lower stiffness. Elbow down limbs were loaded in compression in a hydraulic jig. Axial limb force was measured with a load cell, leg length and tendon strain with a video motion analysis system. The strain experienced by each flexor structure in situ was determined from force length data. Muscle tendon moment arms around the joints under different limb loads were determined from latero-medial radiographs. The SDFT, DDFT, and SL were then removed from the limb and loaded in tension in a hydraulic testing machine using cryoclamps. Their structural stiffness was determined from force-length data and scaled to muscle tendon unit length. Preliminary data show that stiffness of the DDFT and SL varies between different horses, similar to what has been found in the SDFT. There is some evidence that the relative stiffness of the three flexor structures also varies between animals.

A11.30

The hind limb of the horse: spring or motor?

R.C. Payne, J. Robilliard and A.M. Wilson, (Structure and Motion Lab, Royal Veterinary College, UK)

The equine forelimb functions as a linear compression spring during stance phase. Most of the shortening occurs by extension of the metacarpo-phalangeal joint with elongation of long digital flexor muscle-tendon units with short fibres. The hindlimb however, contains most of the propulsive muscle of the horse and it is unclear if a similar arrangement exists. Here we hypothesise that most of the length change for level locomotion occurs in the MTP joint of the hindlimb where there is a similar arrangement of elastic tendons and short muscle fibres and that the more proximal muscles are used for propulsion. Dissection of cadavers demonstrated that the hind legs contained about three times the propulsive mass of the forelimbs. We investigated the relationship between force and MTP joint angle and leg length using a force plate and motion analysis system. During stance the distal limb shortened by about 10% at trot and then lengthened (similar to forelimb), but to greater than initial length. The proximal limb gradually shortened throughout stance as the hip extended. MTP joint extension accounted for most of the leg length change observed, as in the forelimb. A linear relationship was found between MTP angle and limb force at trot ($r^2 = 0.884-0.980$) but less so at walk ($r^2 = 0.640-0.980$). The distal hindlimb therefore acts as a linear compression spring with predominantly passive properties. It is likely that when power production is required (incline and jumping), extension of the muscular proximal limb is used.

A11.31

The biomechanics of the sit-to-stand transition in animals

J.R. Hutchinson, J.J. Robilliard, and A.M. Wilson, (The Royal Veterinary College, London, UK)

Optimisation for walking and running in terrestrial vertebrates has been studied in detail. Economy relies on minimising fibre lengths for economy of force generation, and for achieving length change in passive elastic components of the muscle-tendon units. Animals however also have to go from an upright standing to a crouched sitting position or vice versa. Theoretically, such large-amplitude quasi-static movements might be expected to require extreme length excursions of extensor muscle fibers in particular. This appears to be at odds with the optimal design for efficient locomotion and may represent a design constraint for terrestrial animals. Here we analysed experimental and anatomical data

from representative taxa to determine what length changes muscle-tendon units must achieve in order to execute these motions. The extensor muscle fibers of a horse executing a standing motion with hip and knee joint excursions of 90° and 70° should undergo length changes of about 67 and 78% respectively. Similar results, even up to 100% fiber length changes, are obtained with data from other taxa including humans and birds. Such changes are well beyond the <40% excursions typical of locomoting animals, and are seemingly at a poor position on the force-length curve of the muscles. We discuss how the musculoskeletal system in representative taxa manages these movements, and in turn how anatomical design can limit the range of possible sit-to-stand movements.

A11.32

Characteristics of hoof-ground collisions during locomotion in horses

J Burn, (Anatomy, Bristol, UK)

Collision force occurs between the foot and the ground at the beginning of stance phase during terrestrial locomotion. In humans this force has been measured using force platforms and has been shown to exceed the ground reaction force due to weight-bearing under certain circumstances. In ungulates, the relatively high stiffness of hoof horn prevents the use of commercially available force platforms to measure collision force but collision acceleration can be measured using hoof mounted accelerometers. In this study hoof acceleration in trotting horses was measured for different types of horse shoe and ground surface. It was hypothesised that the magnitude of collision acceleration, and the maximum frequency of hoof vibration following ground contact, would increase with stiffness of the foot-ground interface. Spectral analysis using wavelets was used to decompose the acceleration signal in time and frequency. For all shoe surface combinations, vibrations of the hoof wall following impact dissipated within 50ms. There was a clear positive association between stiffness of the foot-floor interface and both magnitude and frequency of acceleration following foot placement. During this time, the direction of the acceleration vector varied rapidly and randomly over a 360 degree range of angle. It is suggested that structures in the equine foot that function to isolate shock may be adapted to accommodate forces incident from all directions.

A11.33

Comparison of trot and pace in horses

T.H. Witte, T. Pfau, J.J. Robilliard and A.M. Wilson, (Royal Veterinary College, London, UK)

When moving at moderate speed most quadrupeds trot, alternating diagonals pairs of limbs to support the trunk.

Camels, giraffes and some horses and dogs prefer to pace, pairing ipsilateral limbs instead (Hildebrand, 1965). Pacing is suggested to be more efficient due to reduced vertical movement of the centre of mass. Four fit horses that could race at both trot and pace were examined. Stance time was determined from foot mounted accelerometers, speed using a GPS data logger and trunk movement with an inertial sensor mounted over the thoracic spine. Leg angle at foot on and foot off were determined from video data. Horses were driven at gradually increasing speed at each gait. All four horses showed the same pattern, with stance time similar between gaits (176ms; range 168-183ms at pace vs. 163ms; range 168 to 188ms at trot), protraction time was however 13% less and stride frequency 6% higher at pace. Vertical trunk displacement was 7cm (range 5 to 8cm) at trot and 5cm (range 4 to 6cm) at pace. The caudal phase of the stance was longer in pace. Pacing horses thus out-perform trotting horses not by reducing the vertical oscillation of their centre of mass or by increasing stance time/sweep angle but by protracting their limbs more quickly, hence increasing stride frequency and duty factor. The extended caudal phase of the stride results in biceps being stretched further, storing more elastic strain energy and protracting the limb more quickly.

Hildebrand, M. (1965) Symmetrical gaits of horses. *Science* 150, 701-708.

A11.34

High-speed X-ray video analysis of catfish prey capture kinematics

S. Van Wassenbergh, A. Herrel and P. Aerts, (Functional Morphology, Antwerp, Belgium); D. Adriaens, (Vertebrate Morphology, Ghent, Belgium)

The air-breathing catfishes (Clariidae) are a successful and widely distributed group of predatory catfishes. Surprisingly, as for most catfishes, very little is known about the mechanics of feeding in this group of fishes. Previous work has shown that clariid species use suction feeding to draw prey towards and into their buccal cavities. In this study, the rapid internal movement of the bony structures of the expanding cranial system was studied using a high-speed X-ray video system recording prey captures of two *Clarias gariepinus* individuals (250 Hz). The kinematic profiles of a small, marked prey were analyzed as well. In contrast to what has been hypothesized in studies of the cranial morphology of *Clarias gariepinus*, the prey capture kinematics show that this species is an excellent suction feeder. The hyoid apparatus depresses the floor of the mouth by rotations that frequently exceed 50 degrees. Also, a substantial lateral expansion of the suspensoria, by which the hyoid bars and left and right lower jaws are abducted, is

observed. The prey is accelerated to considerably high velocities (1.2 m/s) when it is sucked through the buccal cavity. Peak prey velocity is reached almost exactly at the moment at which mouth opening and the speed of hyoid expansion are maximal.

A11.35

Muscular gating of phonation in birdsong: The ringneck dove (*Streptopelia risoria*)

C.P.H. Elemans, I.L.Y. Spierts, J.L. van Leeuwen, (Wageningen University, the Netherlands) and F. Goller, (University of Utah, USA)

Birds are capable of generating a spectacular range of songs. This is a result of the neuromuscular control and intrinsic properties of the syrinx, a vocal organ unique to birds. Sound is generated by flow-induced oscillation of membranes or labia in the syrinx. In ringneck doves, the coo consists of two separate sound elements. The start of the second element, the trill, is strongly amplitude-modulated at a rate of about 20 Hz. The fast gating of sound during the trill is thought to be controlled by a yet unidentified valve system. Two paired, antagonistic muscles [mm. tracheolateralis (TL) and mm. sternotrachealis (ST)], affect the position of the vibrating membranes. The TL run along both sides of the trachea and insert directly on the membranes. We tested whether control of the membranes by the syringeal muscles is fast enough to gate the trill. We recorded EMG activity in spontaneous vocalisations and measured isometric and dynamic muscle properties in vitro. EMG measurements showed that the TL were active during both sound elements and exhibited strong pulsatile activity during the trill. In vitro isometric properties showed that both TL and ST are relatively fast muscles with response times in the order of 5 ms. The TL produce optimal power output at cycle frequencies of about 20 Hz which match the trill rate in the coo. The syringeal muscles generate forces fast enough to gate sound production. To achieve these contraction speeds, they require extreme muscle properties characteristic of very fast muscles.

A11.36

Bone strains in the emu hindlimb through ontogeny

R.P. Main and A.A. Biewener, (Harvard University, USA)

How do strains in the skeletal elements of a limb change as an animal increases in size and mass through ontogeny? The rules of scaling imply that if a bone's cross-section supporting the weight of the animal grows isometrically, strains would increase with size as the animal's mass increases disproportionately to the cross-section of the bone. The theory of dynamic strain similarity,

however, states that regardless of size, strains in the limb element will remain constant, presumably due to a departure from isometry in ontogenetic bone growth and/or a change in the animal's behaviour or posture, and therefore, a change in the way the limb is loaded. Using emu (*Dromaius novaehollandiae*), this study's aim was to determine how limb loading, kinematics, and bone geometry relate to ontogenetic patterns of bone strain. This was done through the examination of ground reaction forces (GRF), in vivo bone strain measurements in the femur and tibiotarsus, and bone morphology, specifically cross-sectional bone geometry. Although relative limb loads did not change significantly throughout ontogeny, bone strains in the femur and tibiotarsus increased for both walking and running gaits with an ontogenetic increase in mass. It was interesting that strains increased through ontogeny even though measurements of the diameters of these two bones showed positive ontogenetic allometry. Future measurements of these bones' cross-sectional geometry may help explain why the increase in strains occurred.

A11.37

Dynamic wing shape in flying insects: Unraveling the contributions of wing structure and flight forces

S.A. Combes, (University of Washington, USA)

During flapping flight, insect wings deform passively in response to the dynamic forces acting upon them. Although the three-dimensional shape of wings can have a large effect on force production, wing flexibility is often overlooked in models of insect flight, both because measurements of the structural characteristics that control wing bending are rare, and because the relative importance of various flight forces in determining wing deformations remains unclear. I use a combination of experimental and computational approaches to examine the contributions of wing structure and flight forces to dynamic wing shape. First, I measure flexural stiffness and quantify patterns of supporting veins in 16 insect species. I find that average spanwise and chordwise stiffness scale strongly with wing size, but are unrelated to wing venation traits. Next, I estimate the spatial pattern of flexural stiffness variation in the wings of hawkmoths and dragonflies, and find that stiffness declines exponentially in both insects. Finite element models suggest that this stiffness pattern localizes passive bending to the edges of the wing. Finally, I explore the relative contributions of aerodynamic and inertial-elastic forces to wing deformations by comparing bending in fresh hawkmoth wings flapped in normal air versus helium (15% air density). I find that a substantial reduction in air density produces only slight changes in bending patterns. Therefore, a finite element model may be able to

predict patterns of wing deformation independent of aerodynamic force production, greatly simplifying the task of incorporating dynamic wing shape changes into models of insect flight.

A11.38

Daddy-long-legs: Structure, materials and functioning of a particularly twisty insect wing

R.J. Wootton and I.C. Hunt, (Biological Sciences, Exeter, UK)

Many insects, including most flies, twist the wings in flight through large angles around the longitudinal axis, so gaining upward, weight-supporting forces during the morphological upstroke. As the wings are hinged, not pivoted to the thorax they need to undergo elastic torsion within their length. In most flies, and many other insects, this is facilitated by a weakly supported trailing edge. The wing of a crane fly (Tipulidae), however, has a long, stiff, posterior supporting spar, and torsion presents interesting mechanical problems. These, and their solutions, are investigated using progressively realistic physical models and detailed examination of the wings' structure and of the ultrastructure of their cuticle.

A11.39

Aerodynamics and wake structures of a flapping wing model

T. Hubel and C. Tropea, (Fluid mechanics and aerodynamics, University of Darmstadt, Germany)

In the present study a flapping wing model with a Reynolds number of $Re = \rho U c / \eta = 90,000$ and a reduced frequency of $k = fc / (2U) = 0.09 - 0.18$ has been experimentally investigated in the large (2.2m x 2.9m), low-speed wind tunnel of the Technical University of Darmstadt. (U – flow velocity, c – chord of wing, f – frequency of wingbeat). This model corresponds to the aerodynamic characteristics of a goose. Previous observations have postulated three possible gaits for such birds: a ladder structure of vortices in the wake, a continuous vortex gait in cruising flight and a vortex-ring gait in slow flight. The former two differ only in that the overall circulation (lift) varies throughout one wingbeat cycle, leaving a start and stop transverse vortex in the wake. The purpose of the present study is to experimentally investigate which flight parameters influence the change of circulation. Particle image velocimetry is used for flowfield measurements and visualization, synchronized with the wingbeat. Measurement planes parallel to the flow direction and perpendicular to the flow direction are used to visualize both shed vortices from the wing trailing edge and the tip vortices in the far-field wake. Parallel to these wake measurements a three-com-

ponent balance records time-resolved forces acting on the model are planned. The results reveal not only the overall lift, but also its distribution over the wing throughout the wingbeat. These are investigated as a function of reduced frequency, amplitude of flapping and angle of attack.

A11.40

Direct pressure measurements along bird wings during steady flapping flight

J.R. Usherwood and A.A. Biewener, (Harvard University, USA)

Direct pressure measurements from electronic pressure transducers allow new insight into many aspects of bird flight. However, the relatively low-pressure signals and high accelerations of the flight surfaces of birds present a number of challenges to these techniques. We discuss the merits and limitations to acceleration compensation via two methods: paired absolute pressure sensors, in which the differential signal between upper and lower surfaces cancel the acceleration component; and differential pressure sensors linked to single-axis accelerometers. We describe attachment techniques allowing transducer placement across single feathers, and justify the techniques by relating pressure maps to measurements of wing loading using separated, dried wings attached to force transducers in a windtunnel. Dynamic pressure maps for wings and tail of flapping birds allow inferences concerning unsteady aerodynamic mechanisms, wing-tail interactions and inertial power management. Pressure and acceleration maps for pigeons in take-off, level and landing flight show pressure peaks relating to both velocity and acceleration peaks, showing the influence of 'added mass' accelerations. In addition, the influence of the wings on the pressures experienced by the tail can be separated into two components: the interaction between the pressure field associated with the wing near mid-downstroke appears to cause a pressure peak at the tail; and the strong deceleration of the wings at the end of downstroke is related to an acceleration of the tail forwards and downwards (associated with a pressure peak directed dorsally), probably due to purely inertial considerations.

A11.41

Dynamic flight forces in the Desert Locust: stability of a periodic system

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Most forms of animal locomotion are oscillatory. This opens avenues for analysis that capture the oscillatory dynamics of the system, and exploit their periodicity in

formulating the equations of motion. Using dynamic force-moment data from statically tethered Desert Locusts *Schistocerca gregaria*, we first explore how the total aerodynamic and inertial forces vary periodically through the locust wingbeat. We next consider how the periodic forces vary with changes in speed and body angle, fitting Fourier series approximations to each force-moment component in each test condition. The Fourier series approximations are then used to calculate the instantaneous forces and moments at multiple points through the stroke cycle. A linear regression with respect to speed and body angle is fitted to the force-moment data at every point through the stroke cycle, and a Fourier series approximation is used to describe how the slopes of the regressions vary through the wingbeat. The resulting equations are used to provide periodic coefficients for populating the system matrix, giving the first periodic models of stability in flapping flight. This allows us to find analytical solutions to the linearized periodic equations of motion, and numerical solutions to the non-linear periodic equations of motion. This represents a substantial advance over the first generation of semi-empirical models of flapping flight stability. These used quasi-static coefficients and therefore failed to capture the periodic forcing of the flight dynamics. In principle, the same basic tools of linear periodic analysis can be applied to oscillatory locomotion in general, including walking, running and swimming.

A11.42

How small can flying insects get without resorting to asynchronous flight muscle?

L. Maskell and R.J. Wootton, (Biological Sciences, Exeter University, UK)

Asynchronous, stretch-activated flight muscle, capable of contracting many times per nerve impulse, has arisen independently at least eight times within the insects, and has repeatedly allowed the evolution of tiny forms with necessarily high wing-beat frequencies. But how small can insects be without it? Asynchronous muscle has never been found in the Amphiesmenoptera—the superorder comprising the moths, butterflies and caddises; yet some moths are minute, with wing-spans as low as 3mm. We have examined the flight muscle ultrastructure, wing loading and wing-beat frequency of the nepticid moth *Ectoedemia septembrella*. The muscle proves to be of the close-packed, synchronous histological type and frequencies are within the accepted range for synchronous muscle, despite the insects' small size. Flies, wasps and bugs of comparable size have far higher frequencies - and asynchronous muscle.

How does *Ectoedemia*, and by implication even smaller nepticulids, fly with stroke frequencies in the synchronous range? Its wing loading, calculated assuming that the marginal fringe of bristles acts as a continuous sur-

face, is unexceptional among insects of this size. An aerodynamic explanation seems necessary—but nepticulid kinematics are unknown.

A11.43

Low-speed maneuvering flight in the rose-breasted cockatoo

T.L. Hedrick, J.R. Usherwood, A.A. Biewener, (OEB, Harvard University, USA)

We investigated the neuromuscular control and flight kinematics of rose-breasted cockatoos (*Eolophus roseicapillus*, n=6) trained to execute low-speed 90-degree turns in a flight corridor. We recorded electromyograms (EMGs) from both pectoralis, supracoracoideus, biceps brachii and extensor metacarpi radialis muscles along with 250 Hz high-speed 3D kinematics. The cockatoos performed a banked turn with a mean flight velocity of 2.9 m/s and a mean yaw rate of 147 degrees/s. The cockatoos tended to maintain potential energy through the turn while kinetic energy decreased slightly prior to the turn and increased again midway through the maneuver. Based on prior studies of low speed avian turning we hypothesized that turns would be initiated and controlled by bilateral differences in muscle activation timing. However, we found only small bilateral differences in EMG timing, these ranged from 0.6 to 3.5 % of the EMG burst duration and do not appear to be a significant factor in the initiation and control of turns. We found wide variation in the EMG burst amplitude through time as the cockatoos maneuvered through the flight corridor. However, despite the modulation of EMG amplitude through time we found no significant bilateral modulation between the left and right pectoralis or supracoracoideus. We did find significant differences between the left and right biceps brachii and extensor metacarpi radialis muscles and conclude that the cockatoos initiate and control turns by changing the properties of the airfoil such as overall length and angle of attack. (Supported by NSF IBN-0090265)

A11.44

Differential pressure as a tool to investigate fish physiology and behaviour

R.S. Ferrari (IMC-International Marine Centre, Italy); D.M. Webber, (VEMCO, Canada); C. Lefrançois, A. Satta, (IMC, Italy) and P. Domenici, (CNR, Italy)

This study was aimed at employing miniature differential pressure sensors to investigate fish swimming energetics. Previous studies carried out in two species (cod and seabass) showed that caudal differential pressure is a good estimator of the power generated by fish to swim at a given velocity. Recent studies have also shown that

pressure generated by the tail is highly correlated to oxygen consumption of axial muscles of flatfish (flounder) and cod. The present study was aimed at employing differential pressure sensors in order to (1) investigate energy saving of grey mullets swimming in a school and (2) to explore the use of opercular pressure as a predictor of oxygen consumption in round fish (grey mullet). Fish were swam in a swimming respirometer using a step-protocol involving regular velocity increments. In the schooling experiment, fish were swum in pairs each individual with a pressure sensor mounted on the caudal fin. Their relative positions and caudal fin oscillations were measured from video images of the lateral and dorsal undulations of the tail. In the oxygen consumption experiment, the pressure sensor was positioned near the opercula and a tube was extended from the pressure sensor close to the gills. Fish were individually swum and oxygen consumption (M_{O_2}) was monitored after each speed increment. The feasibility of using differential pressure as a tool to estimate energy saving in schools and aerobic metabolic rate of round fish will be discussed.

A11.45

Biomechanics of jumping in *Drosophila*

N. Zumstein, O. Forman, U. Nongthomba, J.C. Sparrow and C.J.H. Elliott (University of York, UK)

We measured the distances jumped and force produced by the main jumping muscle, the tergotrochanteral muscle (TTM) in 2 wild type *Drosophila* strains (Canton-S and Texas) and in m18 and *hono* mutants. After removing the wings, female Canton-S and Texas wild type strains jumped 28.6 ± 0.7 and 30.2 ± 1.0 (mean \pm SE) mm. The males did not jump significantly differently, even though they are lighter. Female m18 and *hono* mutants jump 20.7 ± 0.7 and 20.7 ± 0.4 mm respectively. The peak force produced in female Canton-S and Texas by the TTM is 101 ± 4.4 μ N, for femur-tibia joint angles in the range 90–120°, but declines as the leg is extended further. The force of the TTM in m18 and *hono* mutants is significantly less than the wild type at 52% and 55% respectively. For a female wild type *Drosophila*, jumping 30mm corresponds to a KE of 200nJ on take-off (allowing 20% of the energy to overcome air resistance). We develop equations of motion for a linear force-time model of take-off and calculate that the time to take off is 4.9ms and the peak force should be 264 μ N (132 μ N /leg). We conclude that the fly does not need to store large quantities of elastic energy in order to make its jump. From the reduced distance and force production in m18, a mutant deficient in octopamine synthesis, and in *hono*, a tyramine/octopamine receptor mutant, we conclude that, as in locusts, in *Drosophila* octopamine modulates escape jumping.

A11.46

Attachment forces of the hemelytra-locking mechanisms in aquatic bugs (Heteroptera: Belostomatidae)

P.J. Perez Goodwyn and Stanislav N. Gorb, (Evolutionary Biomaterials, Stuttgart, Germany)

Combined hemelytra-locking system of Heteroptera, consisting of several locking mechanisms, aids the mechanical stabilisation of the body at rest, resists external loads, and keeps air stored with the option to easily unlock hemelytra prior to flight. The resistance to unlocking of the hemelytron was measured (in mN) with the aid of a load cell force transducer combined with a three-axial micromanipulator. It is shown that macro- and microstructural features of several submechanisms are responsible for their directionality. The highest resistance to unlocking was measured in lateral and dorsal directions. Summarised force of separately measured submechanisms was considerably lower than the force measured in the combined mechanism. Each submechanism is optimised for achieving high resistance to the hemelytron uncoupling in particular direction(s) and to be easily unlocked in another direction. It was demonstrated in the high-speed video recordings that hemelytra uncoupling is promoted by their short anterior displacement.

A11.47

Flow patterns around swift wings

J.J. Videler and E.J. Stamhuis, (Groningen University, The Netherlands)

Swifts (*Apus apus*) are extremely aerial birds ultimately adapted to stay airborne. They fly day and night, forage and copulate on the wings, and are long distance annual migrants. Special adaptations include a well streamlined body and tail and long scythe shaped wings. The hand wings are extremely large occupying about 75 % of the total wing length. We tested the flow pattern around a swift wing model with adjustable sweep back angle of the hand wing in a water tunnel using dye and particle image velocimetry to visualise the flow. The flow velocity was about 0.5 m s⁻¹. The model wing had the size of a real swift wing and was made of brass. The hand wing part could rotate around the position of the centre of the wrist joint in the real bird. The short arm part was slightly cambered following the centre of the natural cross sectional profile of the real wing. Series of sweep angles between 0° (straight wing) and 60° (maximum angle) were tested using 5° increments for angles of attack of 12° and 22° (measured at the point of attachment of the wing to the wall of the flume). A conventional wing flow pattern is found around the straight

wing: the flow remains attached and a vortex emerges at the wing tip. The development of a leading edge vortex on the hand wing with increasing sweep back angle will be discussed.

A11.48

Exploring the toughness of feather keratin

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We present new data on the fracture toughness of feather keratin, derived from cutting tests. Rather than use instrumented scissors, we adopted a methodology based on using sprung toenail clippers mounted in a universal test machine. This approach removes the effect of blade-on-blade contact friction from tests, simplifying calculation of cutting energy data. Additionally, the cutting length and geometry remains constant throughout the test, in contrast to the more complicated situation arising when using scissors. We have used this approach to explore regional anisotropies in properties, the effect of pigmentation and the influence of hydration on toughness. These data will enable us to understand how the toughness properties of the composite act to control the robustness of feathers.

A11.49

Gliding flight in the Megachiroptera

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To date, work on bat flight has been largely restricted to kinematic and theoretical analyses. With current interest in the development of flexible-wing Micro-Air Vehicles (MAVs), research into the aerodynamic performance of membranous wings is essential. Empirical measurements of force production during flight in the Chiroptera are therefore needed. Such research would complement recent work on Pterosaur flight, and give an insight into the performance of membranous wings over the entire range of Reynolds number (Re) relevant to vertebrate flight. Bat wings operate at Re between 40 000 and 50 000, where the transition from laminar to turbulent flow occurs. Accurate measurement of aerodynamic force within this transition regime is difficult. Studies of gliding flight provide a platform from which an accurate analysis of flapping flight can be made. Megabats, known to glide for a more substantial part of their flight time than microbats, are ideal model species. Wing models based upon the morphological characteristics of two species of megabat, *Rousettus aegyptiacus* and *Pteropus rodricensis*, can be tested for aerodynamic force production in a wind tunnel. Kinematic analysis of these species in gliding flight provides a useful cross-check for force measurements. Such glide data provides a start-

ing point for further probing into the aerodynamic performance of the bat wing.

A11.50

Influence of airfoil shape on dynamic insect wing performance

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The membranous airfoils of insects are mostly sharp and corrugated. The airfoils applied in numerical simulations of insect flight, however, are often thick with an unnatural blunt leading edge and in some cases also a blunt trailing edge. Flat and cambered thin plates have also been used in experimental insect models. None of these airfoils truly resemble a real insect airfoil. The main question of the present research is therefore: How significant is the influence of airfoil shape on performance in insect flight? Six airfoils were used to investigate the shape sensitivity with a simple 2D plunging airfoil model for the fruit fly '*Drosophila Melanogaster*' in forward flapping flight. The Reynolds number is equal to 192, the Strouhal number is 0.25 and the dimensionless amplitude is 1.5. The two-dimensional unsteady incompressible flow is computed with a verified and validated Navier-Stokes solver with respect to a non-inertial coordinate system attached to the plunging airfoil. The influence of airfoil shape on flow patterns, the normal force versus tangential force phase diagram and the stroke averaged thrust and efficiency were investigated. The airfoils considered were: A 10% thick ellipse & Naca 0010, a 2% thick ellipse & Naca0002, Naca 4702 and a dragonfly airfoil. It was found that the large-scale vortical flow is independent of airfoil shape whereas the phase diagram and flight performance strongly depends on shape. We therefore conclude that airfoil shape cannot be neglected with respect to performance while it is of secondary importance for the study of vortical wake patterns in insect flight.

A11.51

A kinematic analysis of ants running at different inclinations

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Foraging ants have an astonishing ability to orient themselves in an unknown environment using path integration. It is also known that ants can monitor inclinations and incorporate this information into their distance estimation. The currently most preferred theory states that this distance estimation is mediated through path integration by proprioceptive information processing. Therefore the ants must be able to calculate both step length

and inclination. In order to clarify the mechanisms lying behind these impressive abilities we intend to analyse kinematics and dynamics of ant locomotion. In a first step we investigated the two-dimensional kinematics of wood ants, *Formica praetensis*, by focusing on parameters such as speed, step length, duty factor and footfall geometry at different inclinations (0° , $\pm 30^\circ$, $\pm 60^\circ$). In the laboratory ants were trained to forage to a feeder located about 4 m away from the nest at the end of an aluminium channel. A section of this channel could be altered in its inclination allowing high-speed recordings on freely running ants. Preliminary data indicate changes in locomotor behaviour only at higher inclinations (60°). While average speed is constant at inclinations between -30° , 0° and 30° , it decreases at steeper paths. Whether this difference is due to stability demands remains to be elucidated.

A11.52

Experimental and analytical study of schooling motion of fish based on two essential individual motions for school formation: approaching motion and parallel orientating motion

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Experimental and analytical study of schooling motion of fish was done focusing on two essential motions (approaching motion, or AM and parallel orientating motion, or POM) for fish to form and maintain a highly organized schooling motion. Two species of fish (bearded silverside, *Atherion elymus*; and striped mullet, or *Mugil cephalus*) was observed and the correlation of measured motion parameters (position, body direction, and moving direction) among individuals was used to determine which motion, AM or POM, each individual was executing. Conspicuous similarities and differences were found between two motions with regard to the number of interacting neighbors, relative position and time delay of motion between interacting individuals, and analytical model to simulate schooling motion was designed based on those experimental results. The simulated schooling motion showed large similarity to the motion of natural fish school and was used to study the relationship between local interaction among individuals and global properties of schooling motion. Thus, the property of schooling motion based on AM and POM was clarified both quantitatively and qualitatively by the experimental and analytical approach.

A11.53

Ontogeny and mechanical properties of dolphin bone as evidenced by indentation

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On a sample of 25 males and 25 females of striped dolphin (*Stenella coeruleoalba*) radius cross-sections at midshaft were obtained. On these cross-sections, micro and nanohardness were measured with an INDENTEC machine. Indentation was carried out on different points on centre and outer of the sections: nine different positions for microindentation and six positions for nanoindentation. Since age was known for all the animals, exponential equations were separately calculated for females and males, and for each topological position, using Gompertz function. The confidence intervals calculated for the different parameters of the equations showed that no significant difference existed between sexes, whatever the zone of the section on which the test was done. These results evidenced that mechanically the growth model of dolphin bone, which involves the apparition of a cancellous structure, is independent of sex.

A11.54

Measurement of kinematics and computational modeling of dynamics in a freely flying insect

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A robust measurement technique for determining the freely flying kinematics is described firstly. The method is derived from optical triangulation and based on a projected comb-fringe technique combined with the natural or artificial landmarks on an insect, allowing us to establish the local body-centered coordinate system with high accuracy, and to measure the body attitude at any instant. The flying kinematic parameters, including wingbeat frequency, flapping angle, angle of attack, torsional angle and camber deformation, required no assumptions with respect to wing geometry, deformability (except the assumption of rigid leading edges) or bilateral wing symmetry, and the parameters of body position and attitude can be obtained simultaneously by calculation. Based on the kinematics data obtained by measurement and analysis, an integrated computational dynamic simulator was developed then. The simulator is designed for a flexible multi-body system, which is capable to mimic the free flights involving hovering, forward flight and turning maneuvers. Two typical flight behaviors, forward flight and turning maneuvers, of dragonflies Poly-

canthagyna melanictera Selys were analyzed and revealed that the present methods show great potential in modeling dynamics of a freely flying insect.

A11.55

Directionally compliant legs influence passive pitch behavior of a trotting quadruped model

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In trotting animals, the forelimbs exert a net braking force while the hindlimbs exert a net propulsive force. This pattern has been observed in quadrupeds and hexapods alike. Here, I present a quadrupedal trotting model in which forelimb braking and hindlimb propulsion were achieved with directionally compliant legs, where the leg design itself imparted a braking or propulsive force bias. Directional compliance was built into the legs by using a compliant prismatic (telescoping) joint in the distal leg segment, which was connected to a rigid proximal leg segment by a compliant 'knee'. A forward-pointing knee produced a propulsive force bias, while a rearward-pointing knee produced a braking force bias. Trotting was simulated in two models with opposite leg configurations. Model I used forward-pointing knees in the hindlegs and rearward-pointing knees in the forelegs (resembling knees and elbows of quadrupeds) and Model II used forward-pointing knees in the forelegs and rearward pointing knees in the hindlegs. Simulations revealed minimal pitch oscillations during steady-speed trotting of Model I, but substantially greater and more irregular pitch oscillations of Model II. In Model I, intrinsic foreleg and hindleg forces reduced pitching moments during early and late stance. This passive mechanism for minimizing pitch oscillations is an emergent property of directionally compliant legs with the fore-hind configuration of Model I. Such intrinsic stability resulting from mechanical design can simplify control tasks and lead to more robust running machines, as well as an improved understanding of leg design in animals

A11.56

"Ready for touch-down" – Flatfish gliding downwards

R.Gesser, E.J. Stamhuis and J.J. Videler, (Dept. of Marine Biology, University of Groningen, The Netherlands)

Juvenile flounders (*Platichthys flesus* L.) in an experimental tank swim up and down the water column. When

descending they often do not swim downwards but show a distinct downward gliding behaviour. The flatfish bend the tail upwards and keep this posture while gliding down at a rather steep angle. Here we show quantitative analyses of six examples of this gliding behaviour. Juvenile flounders (11 – 15 mm long) were filmed digitally at 250 fps while gliding downward in particle seeded water. The tank was illuminated with a 1mm-thick LASER sheet for PIV flow analysis. In six films gliding speed v_g , angle of gliding α_g (defined as the angle between the gliding path and the vertical) and the tilt angle of the body α_b (which is the angle between the body and the vertical) were measured. Preliminary results indicate high tilt angles during steep descends. The induced flow was analysed using 2-D Particle Image Velocimetry. The poster will present detailed flow analysis as well as final kinematic parameters.

A11.57

A biomimetic approach to new airflow sensors inspired by crickets

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Crickets have evoked a highly sensitive system to detect small changes of flow in their environment. The adult cricket of the genus *Acheta domesticus* has about 600 to 1000 flow sensors and up to 4000 other mechanoreceptors. The airflow sensors comprise flexible hairs, which are inserted into specialised sockets via a membrane. In case of a change in the flow field around the hair, it acts as a second order lever. Additional information about the magnitude of the change in the environment is picked up by the strain sensors, which are most probably excited by surface strains caused by the hair hitting its socket. The sensitivity of the sensors lies in the range of a displacement of a few nanometres at the base of the hair. A combination of different techniques is used to obtain the necessary information to describe the exact response of *single hairs* to air pressure. Their deflection during flow is captured with a high speed camera before they are further investigated by the scanning electron microscope to acquire precise measurements of their structure and the number of associated strain sensors. Material property data is obtained by nanoindentation. All results are integrated into a 3D-model for finite element analysis. This allows us to make simple predictions about the flow sensor's behaviour during a change in its environment. Better understanding of the behaviour of single hairs will be of major importance for building new artificial flow sensors by mimicking a design created by nature.