

## A7–GENERAL BIOMECHANICS

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

### A7.1–Modelling the role of jaw adductor hypertrophy in clariid catfish: effects on bite performance and jaw closing velocity

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Some species of the catfish family Clariidae have unusually large jaw adductors. The hypertrophy of these muscles can potentially increase the performance of two distinct functions of the jaw system during feeding: (1) exerting bite force onto a prey or (2) accelerating the lower jaw resulting in fast snapping of the jaws. In this study, a static bite model and an inverse dynamical model of jaw closing movements were applied to a series of four clariid representatives showing a gradual increase in jaw adductor hypertrophy (*Clarias gariepinus*, *Clariallabes melas*, *Gymnallabes typus* and *Channallabes apus*). The functional properties of the jaw system were measured and high-speed video recordings of prey captures of these 4 species were analysed. The static bite model, in which food reaction forces were calculated in a static force equilibrium, shows that the hypertrophy results in a drastically increased bite force. Closing movements of the lower jaw were modelled as a half-ellipse that rotates in accordance with mouth closings from the high-speed films. The model includes inertia and drag forces on this rotating ellipse. As the peak torque required for these half-ellipse rotations is not higher in the species with increased hypertrophy, our model suggests that the enlarged jaw muscles are not used to generate faster mouth closings. However, individuals of *Clariallabes* and *Gymnallabes* feed at very high gape angles in which the muscular torque of the jaw adductors becomes critically low. Consequently, the hypertrophied jaw adductors could enable these catfish to feed on relatively large prey.

### A7.2–Morphometric differences in skull dimension within Anserinea and the consequences for grazing

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Swans and true geese are phylogenetically closely related. However, their food and feeding behaviour differ;

geese are terrestrial grazers, while swans forage mainly on submerged plants (but also graze on land). During grazing, grassleaves are torn loose by a backward rotation of the head (de Jong unpubl.), mediated by the muscles of the neck. During this movement, grass has to be held firmly between the bills to prevent slipping and the movable upper bill has to counteract the resisting forces of the grass. In birds, a complex system of bones and muscles mediate movement of the upper bill. A 2D-model of this system was used to calculate static bite force at the tip of the bill. Measurements of a mallard were used as starting point. Calculations with this model showed that there are at least three different changes in skull dimensions possible that would increase biting force; 1. decrease in bill length, 2. decrease in skull length, and 3. vertical orientation of the quadrate. Only the first two changes also increase the efficiency of neck muscle forces and increase pulling force. To investigate which of these potential adaptations are present in swans and geese, skull dimensions were measured in all species of these genera. The data show that only the first 2 morphometric changes are found in Anserinae compared to other birds (filterfeeding Anatinae included); the head (geese) and bill length are shorter (geese, swans). These results will be discussed in the context of the hypothetical trophic evolution of anseriforms.

### A7.3–Dynamics and architecture of the chameleon tongue

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The chameleon tongue is well known for its exceptional projection performance. The main constituents of the projectile apparatus are the cylindrical processus entoglossus, a series of nested sheaths with helically arranged collagen fibres that envelop the entoglossus at rest, and a cylindrical accelerator muscle that envelops the sheaths. The inner and outer tubular surfaces of the muscle are covered by a helically arranged epimysium. Previously, we showed that, prior to projection, elastic energy is stored in the collagen structures by the accelerator muscle. During projection, this energy is converted into kinetic energy of the tongue. A forward dynamics model was constructed that predicts quantitatively the elastic energy storage and subsequent projection of the tongue. The model assumes an axisymmetric

arrangement of the structural elements and could therefore be limited to two spatial dimensions. Input of the model is the activation of the muscle fibre system and the structural arrangements and tissue mechanical properties, output is the movement of an array of distributed masses that are accelerated by fibre forces (muscle and connective tissue) and pressure gradient within the tissue. The model demonstrates that the suggested elastic projection mechanism is indeed quantitatively feasible as similar projection performances are obtained as observed on high-speed videos.

#### **A7.4–The effect of manipulation of the moisture content on the mechanical properties of full and partial hoof wall depth samples of donkey hoof horn**

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The inverse relationship between moisture content and the mechanical properties of keratinous materials has not been reported for donkey hoof horn. This study examined, using three point bending tests, the effect of moisture content on the mechanical properties of full and partial hoof wall depth (HWD) samples of donkey hoof horn. A standardised method was used to assess the moisture content of the samples. Full HWD samples were tested at four different levels of hydration: at an in vivo moisture content, following drying over phosphorus pentoxide, fully hydrated and following equilibration at 75% relative humidity. The results indicated that there was an inverse relationship between moisture content and the mechanical properties of donkey hoof horn. There was a significant difference between all data sets ( $p < 0.01$ ) except between those samples tested at an in vivo moisture content and those that were fully hydrated ( $p > 0.05$ ). This may indicate there is a level of hydration beyond which there is no further change in hoof stiffness, thus providing a 'fail safe' mechanism. A stiffness gradient is believed to exist across the full HWD for horse hoof horn. However, previous studies did not control for changes in moisture content across the HWD. A lower moisture content exists in the outer hoof wall compared with the inner hoof wall. In this experiment the full HWD was divided into four sections and samples were tested at the same level of hydration. The results indicated that the mechanical properties did not vary across the four areas tested.

#### **A7.5–Mechanical properties of the solear hoof horn of heifers before and during the first lactation – a prediction of lameness susceptibility**

Betina Winkler, Jean K. Margerison and Charles Brennan, University of Plymouth

Mechanical tests were completed on samples of sole hoof horn taken from 20 heifers at 2 months before parturition (p1) and 100 days postpartum (p2). Simultaneously, all claws were assessed for the lesions score (LS) in the sole horn. Heifers were kept at pasture prepartum and housed loose in a straw bedded yard postpartum. Hoof samples were collected from all claws and analysed for elastic modulus (ELM) and puncture resistance (PR), each measurement was replicated five times on the same area of each claw. Data was analysed by ANOVA – GLM using period and claw as fixed effects. PR force of the sole horn was significantly greater in front claws (FC) when compared to hind claws (HC) ( $P < 0.05$ ) (p1- FC 8.2, HC 7.4N, p2- FC 11.1, HC 10.3N). The PR force and ELM significantly increased postpartum compared with prepartum ( $P < 0.01$ ) (p1- 7.8, p2- 10.7N and p1- 86.9, p2- 118.0N/mm<sup>2</sup>), while the LS of the claw horn increased between periods ( $p < 0.001$ ) (p1- 73.1, p2- 186.5). No significant difference in LS was found between FC and HC in the prepartum period, however LS was significantly greater in the HC compared with the FC in the postpartum period ( $p < 0.001$ ) (HC 223.7, FC 149.3). Prepartum ELM and PR force were not correlated with lesion score either pre or postpartum. However, postpartum ELM and PR force were significantly negatively correlated ( $p < 0.01$ ) to the increase in lesion score between periods ( $R = 0.65$ ). Mechanical tests reflected the changes in housing and in haemorrhage levels that occurred between p1 and p2.

#### **A7.6–Bone strain in the goat radius throughout ontogeny: How in vivo bone strains relate to bone geometry and tissue microstructure**

R.P. Main and A.A. Biewener, Harvard University

For years researchers have examined how the skeletal system accommodates the large size range seen among extant and extinct tetrapods. However, most of these studies have only been concerned with interspecific comparisons. Consequently, little work has examined intraspecific, or ontogenetic, changes in the skeleton as an animal increases in size and mass with age. The goal of the present study was to examine how in vivo bone strain magnitudes and cross-sectional strain distributions compare across different age groups within a species and how these strain patterns reflect the concomitant onto-

genetic changes in bone geometry and tissue structure. We obtained *in vivo* bone strain measurements from the cranial, caudal, and medial surfaces of the radial mid-shaft of young goats at two different ages (4 and 13 wks) over a range of speeds and gaits and compared these with previously published data for adult goats (Biewener and Taylor, 1986). Strain magnitudes were found to be greater in the radii of adult goats at all gaits and gauge locations despite similar ontogenetic limb loading, suggesting possible differences in bone geometry and/or bone tissue properties among the different age classes. Negative allometric scaling of the midshaft cross-sectional area as well as cranio-caudal and medio-lateral second moments of area likely account for the difference observed in strain magnitudes among the different age groups. Other factors such as ontogenetic changes in bone mineral composition and tissue histology will be discussed in relation to these findings.

#### **A7.7—Above ground or below ground? Evolution, canalisation and biomechanics of aerial stems and rhizomes**

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T. Speck, University of Freiburg

Most species of Ranunculaceae are perennial herbs with underground stems, which produce annual axes. *Clematis* belongs to this family and is the only group with a variety of growth forms including plants with rhizomes, lianas and shrubs. We combined biomechanical and anatomical studies to analyse different growth forms of three *Clematis* species, and the mechanical roles of different tissues during development. The study aimed to understand, from an evolutionary perspective, how lianoid forms appeared in *Clematis* and what were the mechanical and evolutionary results of specialization of underground stems in the Ranunculaceae. The biomechanical study revealed three different mechanical patterns during the development of the three species, which varied according to the availability of supports. The secondary growth, which occurs in aerial axes for *C. vitalba* and in underground stems of *C. maritima* and *C. recta*, is responsible for the sloughing of mechanical primary tissues; this process caused a significant fall in structural Young's modulus in older stems. The anatomical structure of rhizomes in the Ranunculaceae includes large parenchyma rays and compliant wood and is not adapted for self-supporting architectures. We hypothesise that woody aerial forms in *Clematis* (lianas) resulted from modification of growth forms with underground stems; this may explain the non-self-supporting derived growth forms in *Clematis*. Specialisation of secondary growth in underground stems within the Ranunculaceae lead to mechanical constraints and canalisation in subsequent

evolution of derived aerial growth forms. These mechanical constraints did not preclude lianescence but lead to a particular type of lianescence in *Clematis*.

#### **A7.8—Anatomy and mechanics of the stem and lateral roots of cleavers (*Galium aparine L.*)**

A. Goodman, Biology, University of Lincoln

Cleavers (*Galium aparine L.*) is a fast growing herbaceous annual with a scrambling-ascending growth habit. Mature plants often use upright species for support and are common in hedgerows and on waste ground. The morphology and mechanics of mature cleavers was investigated using plants grown in pots and ones collected from the grounds at the University of Lincoln, Lincoln, UK. Tensile tests were carried out on the stem and the basal section of the first-order lateral roots. The net orientation of cellulose microfibrils in the cell walls was investigated using polarised light microscopy. Results show that the basal region of the stem and first-order lateral roots was highly extensible. Breaking strains of  $24 \pm 7\%$  were recorded for the stem base and  $28 \pm 6\%$  for the roots. Anatomical observations showed that the basal region of the stem was dominated by a central core of vascular tissue with little or no pith. The net orientation of wall microfibrils in the secondary xylem diverge from the longitudinal by approximately  $9^\circ$ . The mechanism by which the stem is able to withstand such high breaking strains is unclear; reorientation of the cellulose fibrils in the stem along the axis of loading is not thought to be exclusively responsible. Biomechanical data are further discussed with reference to the plant's growth habit and mechanical environment.

#### **A7.9—A mechanical study of retting in Flax (*Linum usitatissimum L.*) and Hemp (*Canabis sativa L.*) stems**

I. Booth, Textiles, De Montfort University; A. M. Goodman, Biology, University of Lincoln

Flax and hemp produce phloem fibres towards the periphery of their stems; individual fibre cells are cemented into discrete bundles around the xylem core by a complex matrix of pectins, hemi-celluloses and lignin. Extraction of undamaged fibres from this structure is critical in successful fibre production. Typically, the cut stems are laid on the ground in swaths for several weeks, where aerobic fungi colonize the senescing stem and hydrolytic enzymes digest the fibre-bundle matrix (dew-retting). More recently, flax stems have been chemically desiccated and the fibre-bundle matrix digested in the standing crop, prior to cutting (stand-retting). Dew-retted hemp stems were clamped horizontally into the jaws of a tensile testing machine and the

work required to remove a strip of fibre-containing peel from the xylem core was measured. A similar investigation was carried out on desiccated flax stems, but samples were clamped vertically due to their finer diameters. Results show an initial increase in the work to peel associated with the dehydration of the stems, from 185–210 J/m<sup>2</sup> in dew-retted hemp and 210–540 J/m<sup>2</sup> in desiccated flax. In both cases this initial increase was followed by a 45% reduction in the work to peel during the following 3–4 weeks, despite relatively constant stem moisture content. This is thought to be a result of the retting process. The peel test can be used to monitor changes at the interface between the fibres and the xylem core during retting, allowing the process to be quantified and compared under different production conditions.

#### **A7.10—Strain measurements of angled muscle fibers during swimming in an aquatic salamander *Siren lacertina***

E. Azizi and E.L. Brainerd, Biology, University of Massachusetts Amherst, USA

Despite numerous studies on the mechanics and motor patterns of axial musculature in fishes, a functional understanding of myomere shape and axial muscle architecture has remained elusive. In contrast to the complex, three-dimensional shape of fish myomeres, the trunk myomeres of salamanders have a relatively simple morphology and can serve as a good system for exploring the mechanics of segmented muscle architecture. The lateral hypaxial musculature of salamanders consists of 2–4 muscle layers with varying muscle fiber angles. The varying fiber orientations in these muscle layers have allowed us to explore the relationship between muscle fiber angle, muscle fiber strain and longitudinal segment strain. We used sonomicrometry to measure muscle fiber strain, shortening velocity and longitudinal segment strain in the lateral hypaxial muscle layers of *Siren lacertina* during steady swimming. We combined measurements of fiber angle and in vivo strain with video motion analysis to determine the relationship between muscle fiber architecture, muscle strain and swimming kinematics. Our results show that strain amplification (longitudinal segment strain/muscle fiber strain) increases with increasing muscle fiber angle (as predicted by models of muscle architecture). These findings demonstrate that, relative to longitudinally oriented muscle fibers and for a given muscle fiber strain, angled muscle fibers produce a greater amount of longitudinal segment strain and body curvature. Supported by NSF IBN9875245 to ELB.

#### **A7.11—Muscle fiber angle and strain amplification in segmented musculature**

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The three-dimensional complexity of myomeres and myosepta has made it difficult to develop a comprehensive understanding of the relationship between muscle fiber angulation, connective tissue mechanics, and locomotor function of axial musculature in fishes. Our approach to this problem has been to study a less complex segmented muscle system – the lateral hypaxial musculature (LHM) of salamanders – in which obliquely-oriented muscle fibers are organized into 2–4 planar layers attached to vertically-oriented myosepta. We have developed a planar, isovolumetric model of the LHM, and tested our model using sonomicrometry during steady swimming in an aquatic salamander, *Siren lacertina*. Predicted segment strains did not deviate from mean measured strains by more than 5%, indicating that our model indeed provides an adequate representation of this relatively simple system. Our model differs from previous models of segmented and pinnate musculature by allowing the segment strains in the two dimensions orthogonal to shortening (Poisson's ratios) to vary within the isovolumetric constraint, i.e. we allow the segment to bulge in either the dorsoventral, mediolateral or both dimensions in response to longitudinal shortening. Our model shows that the ratio of these two orthogonal strains strongly affects the magnitude and speed of segment shortening – greater dorsoventral bulging leads to greater longitudinal segment strain for a given amount of muscle fiber strain (strain amplification). The orthogonal bulging ratio is likely to be affected by the stiffness of the myosepta and skin; therefore our model provides an explicit mechanical link between muscle fiber angulation and connective tissue mechanics.

#### **A7.12—In vivo performance of guinea fowl ankle extensors in relation to locomotor mechanics and stabilization**

M. Daley and A. Biewener, Harvard University

We investigate the in vivo force, length and muscle activity patterns of two ankle extensors of the guinea fowl (*Numida meleagris*), the lateral gastrocnemius (LG) and the digital flexor to the lateral toe (DF-IV), during level and incline treadmill locomotion. Our general goal is to determine the capacity of these two muscles for modulating force and work to meet the mechanical demands of level vs. incline locomotion. Both muscles possess a muscle–tendon architecture that favors isometric contractile behavior for economic force

production during level locomotion, similar to the LG of turkeys (Roberts et al., 1997). In contrast to our expectations, we found that the mechanical performance of these two muscles differs considerably during steady level running: the LG operates at low stress and shortens substantially to produce net positive work, while the DF-IV develops high stress and undergoes a stretch–shorten cycle resulting in little net work. Both muscles increase work generation during incline running; however, they produce only 33% of the work expected for their mass. The LG and DF-IV also modulate work performance through different mechanisms. Whereas the LG shortens more and develops more force during incline running, the DF-IV alters the relative phase of force and length change to increase work output. Based on these results, we hypothesize different roles for each muscle in mediating balance and locomotor stability. Continuing work will combine dynamic simulations and perturbation experiments with in vivo recordings to test this hypothesis.

Roberts et al. (1997) *Science* 275: 1113–1115.

#### **A7.13—Capacity of *Tyrannosaurus rex* to generate vertical ground reaction force**

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The ability to locomote depends on generating adequate vertical ground reaction force (VGRF). To quantify the capacity of *Tyrannosaurus* to generate VGRF, we developed a detailed dynamic model comprised of four rigid bodies: trunk, femur, tibiotarsus, and metatarsus segments. The model was actuated by 34 muscles. Musculoskeletal geometry was derived from phylogenetically-constrained reconstructions. Our analysis showed that for straight-legged postures the passive resistance of the skeleton to gravity supported as much as 65% of body weight; however, for more crouched postures, the skeletal joints supported only about 8% of body weight. Several muscles were identified as influential contributors to vertical support. *M. iliotibialis*, *M. ambiens*, and *M. gastrocnemius pars medialis*, which respectively generated ~0.5, ~0.6, and ~0.8 N of VGRF per N of muscle force, made the largest contributions. In a straight-legged posture, simultaneous application of all muscle forces that contributed positively to the VGRF resulted in about 6 N of VGRF for every N of muscle force. In a crouched posture, only about 2 N of VGRF for every N of muscle force was generated. These data indicate that to generate a VGRF of 2.5 times body weight, the level of support required for running, roughly 10% of body mass would have been needed as extensor muscles in each leg for straight-legged postures, and roughly 30% for crouched postures. These findings suggest that if *Tyrannosaurus* ran at all, it did so in a straight-legged posture.

#### **A7.14—Optimisation of muscle energetics: When to activate and when to shorten?**

G.A. Lichtwark, R.C. Woledge, University College London; A.M. Wilson, University College London & Royal Veterinary College

The relationship between power output of a muscle and the energetic cost of achieving this power output are critical to the locomotory potential of an animal. Previously it has been demonstrated that during sinusoidal length changes of muscle fibres, both the efficiency and the power output of that muscle are highly dependent on the stimulus phase (duty cycle) and duration as a fraction of the mechanical cycle and also the frequency of the movement (Curtin and Woledge, 1996, Ettema, 1996). The combination of these parameters that achieves optimal efficiency, power and the relationship between the two is key in understanding deployment of muscles in locomotion. We investigated this relationship by creating a two-element Hill type muscle model with input parameters similar to those obtained experimentally from the dogfish (*Scyliorhinus Canicula*). This model is an extension of that devised by Curtin et al (1998), which predicted power output during various types of contractions. The extension is to allow predictions of energy cost using the observations of Hill (1938), where the total energy rate is well approximated by the ‘maintenance’ heat rate + ‘shortening’ heat rate + ‘work’ rate (a.b. + a.V. + P.V.). We estimated the efficiency of single cycles across a range of frequencies, duty cycles and stimulation durations. The values obtained were compared to the experimental results of Curtin and Woledge (1996) and a good agreement was found, particularly for slower cycles. By varying the duty cycle, stimulus duration, frequency of movement and other activation parameters we were able to find optimal values of both efficiency and power.

Curtin et al (1998), *J. Exp. Biol.* 201: 103–114.

Curtin, N.A. & Woledge, R.C. (1996), *J. Exp. Biol.* 199: 593–601.

Ettema, G.J.C. (1996), *J. Exp. Biol.* 199: 1983–1997.

Hill, A.V. (1938), *Proc. Roy. Soc. B* 126: 136–195.

#### **A7.15—A comparison of sonomicrometry, ultrasonography and cross sectional area measurement for determination of muscle architecture during contraction**

R. Weller, R. Green, G. Lichtwark, R. Woledge and A. Wilson, Royal Veterinary College, University College London

The timing of muscle shortening during locomotion is key in achieving optimum muscle function. Sonomicrometry and ultrasound imaging are both used to deter-

mine fibre length *in vivo*, but they only give data for a slice of the muscle rather than the muscle as a whole. Maintaining probe contact and field of view with ultrasound is also difficult during dynamic movements such as running. Muscles have constant volume therefore cross sectional area is inversely proportional to their length. Measurement of muscle cross sectional area, could therefore be used to determine when a muscle shortens. Here we examined the *triceps surae* muscle of a subject during a range of equivalent isometric contractions at different joint angles using four different imaging techniques (1) within an MRI unit; (2) with a 7.5MHz ultrasound machine, (3) with three rings of nine CODA motion analysis markers around the shank and (4) with skin mounted sonomicrometry crystals. Finally the subject ran on a treadmill with the same motion analysis marker arrangement and the same sonomicrometry crystals. Motion analysis data were somewhat noisy due to marker tracking by three separate motion analysis units. Definition of the segment of the limb occupied by the *triceps surae* and the choice of fixed landmarks is important. Our experimental data demonstrate that this technique is useful for studying *triceps surae* contraction during dynamic activities where other techniques are inappropriate. Whilst sonomicrometry crystals can also be used for the measurement there were some difficulties in maintaining good acoustic coupling.

#### **A7.16—Can the dynamic behaviour of muscle be predicted from conventional force–velocity data?**

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Muscle ‘steady state’ properties are well known from studies of isolated muscle: force for isometric conditions and power output during constant velocity shortening. However, evidence continues to accumulate showing that muscle rarely operate like this *in vivo*. More often muscles are activated so briefly that force does not develop fully, and shortening and lengthening occur at constantly changing velocity. Do the results of conventional physiological studies of ‘steady state’ properties of muscle give a realistic description of this dynamic behaviour? To answer this question we have attempted to predict the time course of force and power output for dynamic conditions: sinusoidal movement with brief stimulation. The predictions are based on a 2-component mechanical model (contractile component and an elasticity in series with it) and a kinetic model of activation. The characteristics of the mechanical model were measured in conventional ‘steady state’ experiments on red fibres isolated from dogfish. The parameters of activa-

tion were chosen to match the time course of isometric tetanic force. Predictions of force and power during sinusoidal movement were compared with observations. The greatest discrepancies between prediction and observation occurred during relaxation. Predictions of force and power during stimulation give a realistic description of *in vivo* dynamic behaviour if contractile properties, elasticity, and activation are all taken into account.

#### **A7.17—The cephalopod beak as a muscle articulation: a novel joint type**

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Movements between links occur at joints. In nature, there are articulated joints and hydrostatic joints. We present a new class of joint: the muscle articulation. Whereas articulated links touch, links of muscle articulations do not. Instead they are embedded in soft tissue, which provides the motive force for a great range of movement. This tissue also bears reactive forces and transmits force between the links. How cephalopod beaks function was unclear because it was difficult to understand how muscles spanning between the beaks could function in both opening and closing. We have identified the buccal mass as a muscle articulation and have experimentally tested this mechanistic model. We first reconstructed the buccal mass anatomy using serial sections. A series of laterally oriented muscle fibres were found that originate on the outside surface of the upper beak and insert on the thin buccal sheath. We believe these fibres function antagonistically with the other mandibular muscles. To test this we conducted electromyographical recording experiments on isolated buccal masses of *Octopus vulgaris*. During spontaneous and stimulated biting movements, we verified that these fibres were active during opening movements and therefore represent the antagonistic element in this muscle articulation. We suspect muscle articulations are present in many other invertebrates, thus they may be important in their ecology, functional morphology, evolution and development. They may also inspire engineers as a novel joint type.

#### **A7.18—The scaling of mechanical power output of the flight muscles during take off in the Phasianidae**

M.P. McGuigan and G.N. Askew, University of Leeds

It has been predicted that mass-specific power decreases with increasing body mass. This is based on the assumption that muscle stress and strain are constant across spe-

cies, and that limb cycle frequency decreases with increasing body mass. Askew et al (2001) demonstrated a tendency for pectoralis muscle mass-specific power output to decrease with increasing body mass across a range of species in the Phasianidae, but some birds decelerated during the flights and may not have been performing maximally. Thus there is uncertainty about the scaling of power with mass. In this study, we filmed grey partridges (*Perdix perdix*), red legged partridges (*Alectoris rufa*), ring necked pheasants (*Phasianus colchicus*) and peafowl (*Pavo cristatus*) performing escape take-off flights and combined this with published data on blue-breasted quail. The movement of the centre of mass was determined in three-dimensions and the kinetic and potential energy required to move the centre of mass were calculated during the aerial phase of the flight. The mass-specific power required to move the centre of mass was similar across the range of body mass (0.04 kg to 4.5 kg) and higher than that previously reported for other members of the Phasianidae of a similar mass (Tobalske and Dial 2000). The decrease in wingbeat frequency with increasing body mass, resulted in an increase in the mass-specific work generated per wingstroke. Askew, G.N., Marsh, R.L. and Ellington, C.P. (2001) *J. Exp. Biol* **204**, 3601–3619. Tobalske, B.W. and Dial, K.P. (2000) *J. Exp. Biol* **203**, 3319–3332.

### A7.19—Intermittent flight as an energy saving mechanism

P.W. Viscardi, G.N. Askew, R.L. Nudds, M.P. McGuigan, J.M.V. Rayner, University of Leeds

Intermittent flight strategies, in particular flap-gliding (undulating) and flap-bounding (bounding), are utilised by a wide range of avian taxa. Several hypotheses have been proposed to explain their use, primarily regarding energetic efficiency. Various models predicting energy savings at particular flight speeds exist, but these models do not agree with the observed use of these strategies. This is due to oversimplification of the dynamics involved, particularly by regarding flight speed as constant. However, our varying speed model for intermittent flight predicts energy savings at a wider range of flight speeds and has been validated for undulating flight in *Sturnus vulgaris* (European starling). Here we present the results of windtunnel experiments in which the wingbeat and flightpath kinematics of *Melopsittacus undulatus* (budgerigar), flying at a range of speeds, are obtained from high speed video footage (50 Hz & 250 Hz). Budgerigars utilise both undulating and bounding flight, often varying between the two as flight speed

changes; such changes are expected as the bird utilises the most efficient strategy for its speed. Duty factor follows a U-shaped curve with flight speed, reflecting the optimisation of flight strategy to minimise mechanical power output at any given speed. Our data support a varying speed model for bounding flight which predicts savings of mechanical power of approximately 15%, suggesting that intermittent flight strategies are primarily utilised as an energy saving mechanism. Additional benefits conferred by intermittent flight are by no means excluded by our conclusions and they may help provide an understanding of the evolution of these strategies.

### A7.20—Does a general morphology grant a suitable performance on different substrates? The case of Tropicurinae lizards

T. Kohlsdorf and C. A. Navas, University of São Paulo, Brazil

Tropicurinae lizards occupy diverse South American habitats, from desert to forested environments, and use a wide range of substrates, such as rocks, sand and trees. Species that preferentially use branches in forest environments exhibit short tails and hind limbs, and those that use mainly tree trunks also have a characteristic morphology. In contrast, all species from open environments exhibit a generalized morphology, even using physically distinct substrates such as rocks and sand. Fine changes in foot morphology, such as finger and nail lengths, are less evident when phylogenetic relationships are considered. The lack of significant morphological differences among species from open environments has at least two possible explanations: (1) a generalized morphology might grant suitable performance on both substrates, (2) physiological and kinematic adaptations could improve performance. Here, we quantified sprint speed of eight Tropicurinae species on sand and rock, and compared absolute jumping performance among species on an obstacle track. Sand and rock species do not differ in sprint speed on either sandy or rocky surfaces. All species are faster on rock, and running speed differences between substrates are similar. Rock species jump more often than sand ones. We hypothesize that these differences in performance are due to changes in muscle physiology that are not coupled with morphological differentiation. Also, phylogenetic analyses using independent contrasts suggest that performance traits are evolutionary plastic: species differ significantly in both types of locomotor tests and large contrasts are found even between sister species.

### A7.21—Physiological basis of interspecific variation in locomotor performance of *Tropidurus* lizards

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An important functional and evolutionary constraint on the vertebrate locomotor system is the trade-off between sprinting and endurance performance. Such a trade-off has previously been demonstrated among species of Lacertid (Vanhooydonck et al., 2001) and *Tropidurus* lizards (Kohlsdorf and Navas, unpublished data), yet the morphological or physiological bases underlying this constraint have not been identified. Among the 23 South American species of *Tropidurus* lizards, the greatest differences in performance were found between two sister-species, *Tropidurus psamonastes* and *T. itambere*, which were the best sprint and endurance performers, respectively. We conducted a series of experiments to determine the physiological characteristics underlying these interspecific differences in sprint and endurance performance. From contractile studies of their iliofibularis muscle using the work-loop technique, we demonstrated there was no significant in vitro differences in maximum power output or fatigue resistance between the sister-taxa. Using open-flow respirometry, we also found no significant differences in maximal oxygen consumption between the species. In contrast, histochemical analyses revealed the best sprinting species (*T. psamonastes*) possessed a significantly higher proportion of fast glycolytic fibers in their iliofibularis muscle than *T. itambere*. Other possible reasons for interspecific differences in locomotor performance may include a greater dependence on hindlimb muscles other than iliofibularis or variation in motivation or locomotor kinematics.

Vanhooydonck, B, Van Damme, R and Aerts, P. (2001). *Evolution* **55**(5), 1040–1048.

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### A7.22—Comparative biomechanical analysis of jumping in *Anolis* lizards

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*Anolis* lizards have been extensively studied in morphology and ecology. Nevertheless, jumping, an important escape response, has rarely been explored. In this

study we use a force plate to investigate the biomechanics of jumping and its ties to ecology and morphology. Twelve species of Caribbean *Anolis* lizards were induced to jump maximally and biomechanical variables were derived. Relevant morphological variables were also measured. In order to escape a predator, one should jump far and fast. How far one jumps depends on the angle and velocity at takeoff; how fast depends on the duration of the jump. We found that animals have three possible ways to tinker with their performance. Species can: I) increase the length of their legs, which will lead to longer jumps; II) increase their acceleration capacity, which will entail longer, faster jumps, and III) adjust the angle of takeoff. Based on theoretical considerations, we predicted that in order to maximise distance, takeoff angle should be 42 degrees. However, on average, species jumped at shallower angles suggesting a compromise between distance and flight time. Including historical relationships in the analyses suggests that evolutionary changes in takeoff angle, hindlimb length and acceleration capacity explain the differences in jumping capacity among Caribbean *Anolis* lizards. Whereas traditionally, *Anolis* lizards have been classified into distinct ecomorphs based on their morphology, ecology and performance, we found that jumping ability is not correlated with ecomorph classification. Rather, ecological aspects such as conspicuousness seem to explain differences in jumping capacity among species.

### A7.23—Dynamic similarity in terrestrial mammals

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Terrestrial mammals show approximate dynamic similarity in a number of locomotor parameters when they travel at speeds corresponding to equal values of the Froude number. For example, the ratios of peak ground reaction force to body weight, stride length to leg length, stance time to stride time and leg shortening to leg length are independent of size. The Froude number therefore provides a useful means of defining equivalent speeds in mammals of different sizes. It can be shown, however, that perfectly geometrically similar mammals could not move in a dynamically similar manner, because the material properties of mammalian tendons do not scale with body mass. We address the question of how terrestrial mammals scale in order to achieve dynamically similar locomotion. Published data on the scaling of limb properties are combined with a simple mechanical model of the limb, in order to predict the scaling of limb stiffness. A spring-mass model is then used to determine the effect of limb stiffness on other locomotor parameters. We propose that allometric scaling of limb muscle moment arms and ground reaction force moment arms (Biewener, 1990. *Science* 250:

1097–1103) is essential for maintaining approximate dynamic similarity in the locomotion of terrestrial mammals. The fact that dynamic similarity in some parameters is maintained by allometric scaling implies that other mechanical parameters will deviate systematically from dynamic similarity. An implication of this is that comparing mammals at equal Froude numbers will not remove all size-dependent effects.

#### **A7.24—Shear forces generated by tree frogs adhering to smooth surfaces: allometry and possible biomimetic implications**

W.J.P. Barnes, C. Oines and M. Riley, I.B.L.S./D.E.E.B, University of Glasgow

Tree frogs are characterised by possession of large disk-like pads on the tip of each toe that aid adhesion to smooth surfaces. In this study of ten species of hylid tree frog on seven different materials, we measure the shear forces parallel to the surface that prevents frogs from sliding at angles of less than 90°. The frog is weighed and placed on a horizontal surface that is slowly rotated from 0° (horizontal), the angle when the frog begins to slip being used to calculate the shear force. Our graphical analyses combine data for different frogs, so that the way in which shear forces scale with the size of the frogs (indicated by their snout/vent length) is apparent. On Perspex, for instance, shear force scales with length to the power 2.70, which is almost identical to the way in which the mass of the frog scales with frog length (length to the power 2.73). Indeed, our measurements on all surfaces indicate that shear force scales with the mass of the frog. A good indication of how well tree frogs resist slipping is provided by the calculation of coefficients of friction. The largest species studied, *Hyla boans* and *Phrynohyas venulosa*, show the highest values (average values across all surfaces of 1.92 and 1.79, respectively). Interestingly, coefficients of friction on rubber, along with those on wood and the underside of leaves, were on average higher than those on other surfaces. Implications of this research for the tyre industry will be discussed.

#### **A7.25—Adhesion in growing tree frogs: solutions to a sticky problem**

J.M. Smith, I.B.L.S./D.E.E.B, University of Glasgow

Tree frogs have been found to utilise wet adhesion to stick to smooth surfaces, using highly specialised toe pads. Their adhesive mechanism depends on surface area, so the system may be expected to have difficulty compensating for the large increase in mass seen in the development from metamorphosis to adulthood. Using the protocol of Emerson & Diehl (1980), adhesive forces

produced by juveniles and adults from nine species of Trinidadian tree frog were investigated. These were correlated with morphometric data from the frogs, in particular changes in weight and toe pad area with growth. The rate of increase in adhesive force production with growth was greater than predicted, being significantly higher than the increase in toe pad area. This may be correlated to increased morphological complexity and increased cell densities seen on pad surfaces in adults in comparison with juveniles. Additionally, the rate of toe pad area increase was significantly greater than that predicted from isometric growth, while body mass increased at a lower rate than expected from isometry, these trends being less pronounced in smaller species. In smaller species, these mechanisms allow adhesive forces to keep pace with the increase in weight, so that fully-grown adults adhere as well as metamorphs. However, in larger species, the increase in adhesive force does not match the weight increase, so adults adhere less well than juveniles.

Emerson, S.B. & Diehl, D. (1980) *Biol. J. Linn. Soc.*, 13, 199–216.

#### **A7.26—Role of the proximal limb in equine locomotion**

J.C. Watson, Mavrommatis S. & Wilson A.M., The Royal Veterinary College

Equine biceps stores elastic energy through the stance phase which is used to initiate limb protraction. When a horse gallops or jumps the limb is accelerated off the ground more rapidly and it achieves a greater kinetic energy. This may be achieved by two mechanisms (1) biceps is stretched further prior to foot off storing more energy (2) biceps stiffness is higher storing more energy. Biceps consists of a substantial internal tendon; a medial head comprising 18mm long fibres and a lateral head comprising 6mm fibres. The muscle tendon unit is some 400mm long so the muscle fibres are in series with a long aponeurosis with significant passive elastic properties. In this study we test the hypothesis that activation of the muscle fibres results in the associated aponeurosis tissue acting as a passive spring in parallel with the internal tendon. One would therefore expect an activated muscle to be stiffer and hence return more energy when released. Five muscles from horses euthanased for other reasons were subjected to cyclical loading at 1Hz in an Instron servo hydraulic materials testing machine. Muscles were electrically activated every second cycle and force length data recorded. Each experiment was completed within 30 minutes of death. The activated muscles were about twice as stiff on both loading and unloading and the energy returned on unloading was approximately double that for the passive state. The short fibred muscles therefore act as a tuneable spring for the limb protraction catapult rather than to directly move the limb.

### A7.27—Movements of the centre of mass of the horse during field exercise

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

The energetic cost of locomotion has been attributed to the cost of generating ground force and stance time duration. In horses, it has been shown that the energetic cost of moving a unit distance reaches a minimum within each gait and the speed at which this minimum occurs coincides with the preferred speed of horses observed in the field (Hoyt and Taylor, 1981). Energetic optimisation of gait pattern is partly explained from the data of Farley and Taylor (1991) who found that the trot-canter gait transition brought about a drop in average peak limb force as measured on an instrumented treadmill. Thus, a mechanical trigger for gait transition was proposed. Force data collected in this lab, however, showed that limb force increases in the non-lead limb and decreases only slightly if at all in the lead leg at the trot-canter transition. The study presented here sets out to explain the difference in limb loading seen in the asymmetrical gait of canter by measurement of vertical movements of the centre of mass of horses during treadmill and over-ground locomotion with the hypothesis that the movement of the trunk is responsible for the difference in limb force between the lead and non-lead legs. In addition, this information provides insights into the other potential method of optimising gait pattern for energetic cost, i.e. minimising external work.

Hoyt, D. & Taylor, C.R. (1981) *Nature* **292** 239–240

Farley, C. & Taylor, C.R. (1991) *Science* **253** 306–308

### A7.28—Hydromechanics of Mayfly larval swimming

J.H. Brackenbury, Anatomy, Cambridge University

The kinematics and hydrodynamics of free-swimming larvae of the Mayfly *Chloen dipterum* were investigated with the aid of a simple wake visualisation technique (tracer dyes). The swimming movement consists of a high-amplitude dorso-ventral undulation and the wake of a continuously swimming insect is a series of single, discrete spherical vortices which are shed alternately to the left and right sides of the swimming line, one for each half-stroke. The vortices propagate to the side at an angle of ca. 80 degrees relative to the rear. Mayfly larvae, like damselfly larvae and eels, produce separate vortices that propagate laterally rather than the reverse von Karman street with its caudally-flowing jet that is characteristic of fish swimming via use of the caudal fin. Mayfly larvae also possess a rapid start manoeuvre which is similar to the rapid C-start of fish and the twist manoeuvre recently described in Damselfly larvae.

### A7.29—The biomechanics of swimming at intermediate Reynolds numbers: undulatory locomotion in ascidian larvae

M.J. McHenry, Harvard University

Our understanding of the hydrodynamics of swimming comes primarily from research on microorganisms, where viscous forces dominate, and adult fish, where inertial forces dominate. Viscous and inertial forces combine to generate propulsive force in the large diversity of larval invertebrates and vertebrates that are intermediate in body size and Reynolds numbers ( $Re$ ) between these two groups. However, it remains unclear to what degree viscous and inertial fluid forces individually contribute to the hydrodynamics of swimming. I experimentally tested quasi-steady and unsteady blade element models of the hydrodynamics of undulatory swimming in the larvae of the ascidian *Botrylloides* sp. (body length = 3 mm,  $Re = 100$ ) by comparing force predictions by these models with the measured forces generated by tethered larvae and by comparing predictions of swimming speed with speed measurements of freely-swimming larvae. Although both models predicted mean forces that were statistically indistinguishable from measurements, the quasi-steady model more accurately predicted the timing of lateral force production and mean swimming speed than the unsteady model. This suggests that unsteady force (i.e. the acceleration reaction) does not play a role in the dynamics of steady undulatory swimming at this scale.

### A7.30—Swimming kinematics and wake of juvenile Flounders (*Platichthys flesus*)

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

The Flounder (*Platichthys flesus*), a typical flatfish, lies on one side of the body and swims by undulating body and tail up and down. Flounders have a distinct flat and wide body shape. Both eyes lie on one side of the body, and the eyeless side is pointing downwards. The blind side also is remarkably flatter than the upper side. The morphology and swimming style are therefore quite different from round fish. In the study presented here, recently metamorphosed juvenile flounders 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. Since Flounders are not neutrally buoyant, the waves will have to produce lift as well as thrust during steady forward swimming. Kinematic results will be pre-

sented, together with our first quantitative data of the flow patterns produced by the flounders, resulting from a Particle Image Velocimetry (PIV) –study.

### **A7.31–Recent developments in computational mechanical modeling of biofluid dynamics**

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Biological system in swimming and flying is, 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. We have proposed a new paradigm of the *simulation-based biological fluid dynamics*, which, by means of computational modeling of biofluid dynamics through faithful reconstruction of morphology and representation of realistic kinematics of individual object, shows great potential to elucidate the physics and mechanisms in the complicated biological fluid phenomena. In this review 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 flying 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).

### **A7.32–Balancing thrust and drag: The hydrodynamics of anguilliform locomotion in steadily swimming eels (*Anguilla rostrata*)**

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

Wake structure and swimming kinematics of steadily swimming eels (*Anguilla rostrata*) were examined to describe the hydrodynamic differences between anguilliform and carangiform locomotion. High-resolution particle imaging velocimetry (PIV) data were collected for 20cm long eels, swimming at 0.5 to 2 lengths  $s^{-1}$ . At all speeds, the wake consists of alternating direction lat-

eral jets, separated by a shear layer. This shear layer is unstable, and rolls up into two separate vortex cores, producing the unlinked rings previously observed in eel wakes. These lateral jets are not produced in carangiform wakes, in part due to shape differences between anguilliform and carangiform swimmers. The jets are produced along the posterior third of the eel’s body, where carangiform swimmers often have a narrow caudal peduncle, preventing these jets in carangiform wakes. Thus, although the modes are kinematically different, shape differences may also be important. No substantial downstream velocity was observed in the wake, indicating that thrust and drag, which must sum to zero on average, also balance smoothly over time. This smooth balance contrasts with previously observed carangiform wakes, in which a downstream jet is usually observed, indicating spatial or temporal asymmetry between thrust and drag. Elongated body theory was used to estimate lateral forces, which agreed well the PIV estimates, and thrust, which was used to calculate efficiency. Hydrodynamic efficiency was approximately 50% at all speeds.

### **A7.33–Under pressure to swim fast – shark myotomal pressure increases with increasing swimming speed**

A.P. Summers, E.G. Drucker, Univ. California – Irvine, and G. Martinez, Univ. New Hampshire

High speed swimming requires a stiff body to maximize thrust delivered along the main axis of the fish. Swiftly swimming bony fishes have few vertebrae (i.e. 22 in marlins), and have significant bony zygapophyses that span the intervertebral joints. The net result is a very stiff vertebral column which provides the requisite whole-body stiffness. Some sharks are remarkably fast swimmers, yet they have a large number (180 precaudal in the mako shark) of discoidal vertebrae that seem ill-suited to resisting flexion. We tested the hypothesis that sharks can dynamically change their body stiffness by pressurizing their thick, inextensible skin. We implanted pressure transducers in the epaxial musculature of spiny dogfish sharks and swam them in a flow tank at speeds from 0.25 to 1.75 body lengths per second. The myomeric pressure varied sinusoidally over the course of a tail beat cycle, from subambient to superambient. The average pressure increased with increasing speeds, and contralateral pressures were 180 degrees out of phase. Our choice of spiny dogfish as a study animal was dictated by availability and willingness to swim in a flume. They are not very fast swimming sharks and we have evidence that they can swim a good deal faster than we could run our flume (3+ bl/s). We would expect that faster swimming sharks such as makos and great whites would be pressurized to a greater extent.

### **A7.34—Unsteady swimming performance in the spiny dogfish**

P. Domenici, IMC, Oristano; E. Standen, UBC, Vancouver and R. Levine, U. Massachusetts, Amherst

Unsteady swimming performance is of fundamental importance both for capturing prey and for escaping from predators. High distance-derived performance (i.e. high speed and acceleration) and high manoeuvrability (i.e. tight turning radii and high turning rates) are considered indicators of high unsteady swimming performance. Previous work on teleosts has shown that unsteady swimming performance can be correlated with certain morphological features, such as large body depth, especially posteriorly. While a great deal of data is available on bony fishes, very little is known about the unsteady swimming performance of cartilaginous fishes. Spiny dogfish (*Squalus acanthias*) ranging from 47 to 72 cm were startled using a mechanical stimulus. Unsteady swimming manoeuvres were recorded using high speed video at 500 frames/s. High manoeuvrability in spiny dogfish is expected, due to the high flexibility associated with a cartilaginous skeleton. On the other hand, based on the posterior lateral depth, acceleration is not expected to be comparatively high. The kinematics of the dogfish startle response will be compared with those of bony fishes. The relationship between distance-derived parameters and manoeuvrability will be discussed and related to morphological features of elasmobranchs.

### **A7.35—Effect of body size on fast-start performance in the Pacific staghorn sculpin, *Leptocottus armatus***

Emily M. Standen, University of British Columbia, Vancouver; Robert P. Levine, Elizabeth L. Brainerd, University of Massachusetts, Amherst; Paolo Domenici, International Marine Center, Loc. Sa Mardini, Italy

The effect of body size on fast-start performance in fishes has received considerable attention the past few decades and has been the basis for interpretations of the scaling of predator–prey interactions. While many of these scaling studies have focused on maneuverability and distance-related measures of performance, other factors such as latency may also be crucial for predicting outcomes of escape responses. To examine the effects of body size on latency, turning and distance-related performance parameters, escapes from 104 Pacific staghorn sculpins, ranging in total length from 2.2 to 25.2 cm (0.11–195 g), were analyzed using high-speed video.

Our results show that latency, maximum velocity and acceleration increased with increasing total length while maximum turning rate decreased with increasing total length. Distance from the stimulus and initial orientation relative to the stimulus had no significant effect on latency or other measures of performance. Previous theories have suggested that acceleration should decrease with size in geometrically similar animals. Therefore, we suggest that the observed increase in acceleration with body size may be explained by allometric growth. Our results show that the scaling of escape success in fish should take into account a number of size-dependent variables, such as timing, turning and distance-related parameters.

### **A7.36—Effect of hypoxia on escape performance in grey mullet**

Christel Lefrançois, Alexandra Shingles and Paolo Domenici, International Marine Centre, Italy

The behavioural processes relevant for the escape response mainly depend on the animal locomotor and sensory performance. Any effect of hypoxia on the mechanisms involved in these performances may affect the outcome of the prey–predator encounters. To assess the effect of oxygen reduction on fish escape responses, we employed an integrative approach considering both kinematics and timing variables. Recent studies showed that fast and slow escape responses may occur as a reaction to a startling stimulus. As intensity of the stimulus largely determined these two types of responses, any possible effect of the hypoxia on the fish acoustic sensitivity could also affect the occurrence of response type and, therefore, locomotor performance during escape. We tested the effect of hypoxia on locomotor parameters, such as cumulative distance, speed and acceleration, as well as on parameters related to the fish sensitivity, such as responsiveness and time latency, which are less commonly considered. Adult grey mullets were individually tested. Experiments were carried out into a circular tank where escape responses were elicited by a mechanical stimulus by triggering the fall of a dummy. To avoid visual stimulation, the dummy pass through a black tube before hitting the water surface. High speed camera (500 frames.sec<sup>-1</sup>) was used to record the fish response. Escape responses of grey mullets were monitored at four different levels of oxygenation: normoxia (above 85% air saturation), 50%, 20% and 10% air saturation. The relationships between the different parameters tested and oxygen saturation will be analysed and discussed.

### **A7.37–Gait transition and oxygen consumption in swimming striped surf perch (*Embiotoca lateralis*)**

M. Cannas, International Marine Centre, Italy; J. Schaefer, University of California, Irvine and J.F. Steffensen, University of Copenhagen, Denmark

Labriform swimmers rely exclusively on pectoral fin locomotion for a wide range of speeds and only employ their caudal fins for burst swimming or at high speeds. The discrete speed at which this shift in swimming mode occurs is termed the gait transition (Up-c). Gait transition is traditionally thought as a threshold point, at which the animal must 'shift gears' to achieve higher speeds. Striped surf perch (*Embiotoca lateralis*) was used as a model of labriform swimmer. A flow-through respirometer/swim tunnel was used to determine the Up-c and to investigate metabolic costs associated with gait transition. Larger fish were found to recruit the tail for manoeuvring at lower swimming speed (SS) due to unsteady swimming, as described in parrotfish. At high SS, fish began to employ the tail in a burst and coast style of swimming that quickly exhausted the fish.

### **A7.38–Visually mediated escape response in staghorn sculpin (*Leptocottus armatus*)**

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Visually-mediated escape responses in fish are triggered when the rate of change of the visual angle subtended by a putative predator frontal profile reaches a certain threshold (the apparent looming threshold, ALT). We investigated the effect of fish size on the timing of the startle responses in *Leptocottus armatus*. Escape responses were triggered visually by a looming object simulated by using black circles of increasing diameters displayed on a computer screen. A significant negative correlation resulted between ALT and fish size meaning that small-sized fish could reduce the risk of predation for a given escape speed. Since performance in acceleration and velocity in escape responses from a standing start do not vary with size, after a relatively short time the distance traveled by the center of mass of two fish of different sizes will be the same. However, larger prey have to travel a longer distance (and so they need more time) in order to position their whole body outside the predator's approaching gape. This may explain the lower ALT (and therefore larger reaction distance) we observed in larger prey.

### **A7.39–Larval development and swimming in flounders: How much does metamorphosis into a flatfish-appearance change the swimming kinematics?**

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

The Flounder (*Platichthys flesus*) is a common flatfish species in the North Sea. The larvae hatch bilateral symmetrical just as normal 'roundfish', but undergo a metamorphosis during the larval development. Approximately 6–8 weeks after hatching the metamorphosis starts. The orientation of the vertebral column rotates 90° laying the animal on one side. The skull twists and deforms, one eye (most often the left eye) grows around the skull to opposite side, while the body widens to the typical flatfish shape. We wanted to know how this rather dramatic change is reflected in the swimming styles and kinematics of the flounder larvae. Freshly hatched larvae were observed and filmed daily. Still pictures were taken for growth measurements and documentation of the larval development. Larvae at the age of approximately 4–5 weeks, just before or at the beginning of metamorphosis, were caught in the field. They were filmed while swimming voluntarily and freely in still water. From the film pictures wave parameters were taken and standardised with respect to the body length to determine differences in swimming kinematics.

### **A7.40–Tubule density at different sample sites around the stratum medium of horse hoof horn**

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Microscopic analysis shows that equine hoof wall is composed of distinct phases of tubular and intertubular horn. The tubule density (TD) of hoof horn is found by ascertaining the number of tubules per unit area and is believed to relate to mechanical properties, resistance to wear, 'quality', hardness and moisture content. The straight grid previously used to ascertain the TD of hoof horn may omit certain tubules on both the inner and outer hoof wall as the wall itself is curved. This study compared the use of straight and curved grids (designed to follow the contour of the wall) to ascertain the TD at the midline dead centre (MDC) of horse hoof horn. The results indicated that there was no difference between the tubule densities found by using either grid. However, the pattern of tubule distribution was not concurrent with previous studies for pony and horse hoof horn. A further experiment was carried out using a

straight grid to ascertain tubule density at three sample sites around the hoof wall. These were MDC, medial and lateral samples. The TD at each site was different ( $p < 0.05$ ). Samples taken from medial sites showed a comparatively lower TD than both remaining sites ( $p < 0.01$ ). TD was ascertained from four equal sections (zones) across the hoof wall. There were differences in the tubule density of the zones between MDC, medial and lateral samples. These results may reflect differences in the mechanical and functional properties of horse hoof horn at these different sites.

#### **A7.41—Geometry and mechanics in dolphin bones. A possible model for osteoporosis**

C. Alba-Fernández, A. Casinos, University of Barcelona; P. Zioupos, Cranfield University

The radii from a sample of 74 specimens, males and females, of *Stenella coeruleoalba*, ranging from new born animals to adults, were studied. Cross-sections at midshaft were obtained and on them cortical area, maximum second moment of area and polar moment were calculated. The three parameters were regressed to total length of the animals, since body masses were not available. While cortical area scaled faster than predicted, both moments did it slower. Complementary to the geometrical analysis, microhardness tests on individual trabeculae were carried out. Mechanical results behaved the same for males and females. Moreover, these results behaved as seen for growing human cancellous bone. At the light of the present study and the previous descriptions on the ontogenetic transformation of compact bone in cancellous bone in dolphin skeleton, the possibility of using it as a model for osteoporosis is assumed.

#### **A7.42—Mechanical properties of the hooks of plant fruits**

E.V. Gorb and S.N. Gorb, Evolutionary Biomaterials Group, Max-Planck-Institute for Metals Research

In many plant species, seeds and fruits are adapted to dispersal by attaching to animals. Attachment may be realised by two special adaptations, such as adhesion by glue or mechanical interlocking. In the latter case, special structures, such as hooks, appear on the fruit surface and provide interlocking with animal fur and feathers. The hooks may have various origin, size, shape, morphology and arrangement on fruits. In the *Galium aparine* plant, small hooks (length: mean = 281.1  $\mu\text{m}$ , SD =

42.2,  $n = 20$ ) with one curved part almost entirely cover the fruit. Using light and scanning electron microscopy, it was found that the hook consists of two distinct parts, a folded base and a hooked cone. The hook is unicellular and hollow, and may be considered as a modified trichome. Using a force measurement device Basalt-BT01, the detachment force of a single hook (mean = 23.23 mN, SD = 8.13,  $n = 50$ ) and its mechanical properties were measured. In spite of visco-elastic properties of the hook material, hooks break when a certain force is applied to the middle of its curved part. Elastic modulus of intact hooks and hooks with an ablated base are significantly different:  $2.02 \pm 1.5$  GPa ( $N = 7$ ,  $n = 48$ ) and  $23.20 \pm 15.73$  GPa ( $N = 5$ ,  $n = 30$ ), respectively. It is concluded that the soft base serves as a joint providing the rotation of the hook and probably better resistance to forces in different directions. This may increase a chance for an initial interlocking of the fruit from different sides and result in a higher attachment force of the entire fruit.

#### **A7.43—Differences in skull morphology and biting force between fringillids and estrildids**

M.A.A. van der Meij and R.G. Bout, IBL, Leiden University, The Netherlands

Finches crack and husk seeds before swallowing the kernel and consist of two groups of birds, fringillids and estrildids. Fringillids husk hard seeds faster than estrildids, but both groups do not differ in their performance on soft seeds. Is this difference in performance related to a difference in biting force e.g. jaw adductor mass? An independent sample of birds (without finches) show an exponent of adductor mass = body mass<sup>0.75</sup>. The estrildids have a scaling exponent of 0.93 and do not significantly differ from the independent sample of birds. Fringillids differ significantly with a scaling exponent of 1.29 (positive allometric growth). With a relatively higher adductor mass for fringillids we expect a higher maximal biting force for fringillids compared to estrildids. Therefore we measured the biting force directly, the results show a significant higher maximal biting force for fringillids. Comparing the cracking performance corrected for the difference in maximal biting force we expect no difference between the two groups of finches. However, with the same maximal biting force fringillids are faster than estrildids. Kinematical analysis shows that fringillids use a different cracking technique compared to estrildids.

#### **A7.44—Ontogenetic study of the bone cross-sectional geometry in the hind limb of the large lizard *Varanus niloticus***

A. Casinos, University of Barcelona; V. de Buffrénil, Muséum, Paris.

Femur, tibia and fibula of a sample of 31 specimens of *Varanus niloticus* were studied. Animals corresponded to different ontogenetic stages, from juveniles to adults. Cross-sections at midshaft were obtained from the three long bones and on the sections cortical surface area, maximum second moment of area and polar moment were calculated by IMAT program. The three geometric parameters were regressed to the body masses of the animals studied, which ranged from 0.5 to 17 kg. All the parameters scaled in the three bones with exponents not significantly different from the values predicted for geometrically similar animals, although some differences existed among the different bones, since parameters scaled always slower in tibia than in femur or fibula.

#### **A7.45—Simulation of a catapult mechanism in the equine forelimb**

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Rapid protraction of the equine forelimb during locomotion is critical in reducing the ground reaction force at high speeds. It has been shown that rapid protraction is initiated by a catapult mechanism (Wilson et al., 2003). During locomotion the *biceps brachii* muscle acts like a catapult that stores energy slowly as it is stretched by the inertial effects of the horse moving forward, and releases this energy when the carpal joint folds. This release of energy effectively protracts the limb. To demonstrate the effect that releasing this energy has on the resultant kinematics of limb, a simple two-dimensional model of the equine forelimb was created. The model consists of 5 rigid segments and a series of spring like structures that simulate the various flexor and extensor tendons of the limb. The *biceps brachii* is modelled as a spring that is stretched by both shoulder flexion and elbow extension. The spring properties are based on the experimental data. Releasing the stretched spring from various degrees of elbow extension provides more energy than is actually needed to protract the limb and as a result damping is required to prevent over extension and flexion at the joints. It is suggested that various muscles, such as the triceps muscle group, may act to absorb some of this energy by contracting eccentrically

during part of the protraction phase. This is supported by muscle activation data.

Wilson et al (2003), Nature, 421:35–36

#### **A7.46—The role of the extrinsic muscles of the thoracic limb in equine locomotion**

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Muscles have two functions in locomotion 1. resist the gravitational and inertial forces 2. absorb/generate power for changes in velocity or altitude. Force is most cheaply generated by a short fibred pennate muscle whilst the maximum power output of a muscle is architecture independent. In this study we tested the hypothesis that there is a functional separation between the anti gravity muscles and the propulsive muscles in the equine forelimb. Measurements of muscle mass and fibre length were made on each extrinsic muscle of the forelimb of six horses euthanased for other reasons. Maximum contraction velocity of equine muscle (brachiocephalicus) was also measured (4 lengths per second) using fresh muscles from other horses. Muscle physiological cross sectional area, maximum isometric force and maximum power production were then calculated. There was a distinct functional separation between muscles optimised for resisting gravity (serratus ventralis thoracis) and those required for moving the limb or the trunk (the other extrinsic muscles). The extrinsic muscles of the forelimb were incapable of generating sufficient power to make any major contribution to the power required for achieving maximum acceleration from standing as measured in trained racehorses. Thus the high power output required for acceleration in racehorses is predominantly provided by other muscles within the locomotor system.

#### **A7.47—Motor Unit Recruitment in Cat Locomotion**

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Mammalian muscle contains motor units with a range of contractile properties. Different locomotor tasks require different motor unit recruitment patterns as previously demonstrated in fish (1, 2). Different types of motor units generate different frequency spectra within a myoelectric spectrum (3). Therefore, the myoelectric signal from mixed mammalian muscle may be used to determine motor unit recruitment patterns. Observations suggest that different types of motor units are recruited at different times within each running stride in man (4),

however, these observations were not directly linked to the force produced or shortening velocity of the muscle fibres. The purpose of this experiment was to test whether spectral properties of the myoelectric signals were related to the force and shortening velocity of the medial gastrocnemius in the cat. Cats were trained to walk on a motor-driven treadmill at different speeds (0.4–1.6 m/s) on slopes of +30°, 0° and –30°. EMG was measured using indwelling, bipolar, fine wire electrodes. Fibre lengths were measured using sonomicrometry crystals. Force was measured using buckle type force transducers. Different myoelectric spectra occurred at different times during each stride in the cat. These observations suggest that different motor units are recruited at different times, and will be discussed in the context of the fibre length and muscle force.

1. Jayne and Lauder (1994) *J. Comp. Physiol. A* 175: 123–131.
2. Rome et al. (1988) *Nature* 333: 824–827.
3. Wakeling et al. (2002) *J. Exp. Biol.* 205: 359–369.
4. Wakeling et al. (2001) *Eur. J. Appl. Physiol.* 86:40–47.

#### A7.48—Fast Locomotion in spiders

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Spiders use hemolymph pressure for leg extension. The role of hydraulic extension during fast escape maneuvers has been investigated for the example of the hunting spider *Cupiennius salei* Keys. (Arachnidae). Kinematics and dynamics of *C. salei* (n=3, mean mass=4.5g) was observed during induced escape maneuvers. The kinematics was observed with an infrared high-speed camera system; hence reflective markers were affixed at the spiders. For the measurement of the forces we used a self-made three-dimensional force plate (resolution:  $\pm 0.3$  mN). The maximum velocities of the animals reached up to 480 mm/s. Escape velocities of approx. 200 mm/s are preferred. The fourth leg produced with 53% (n=23) the main fraction of the vertical ground-reaction-forces, the third leg 33% (n=13), the second 17% (n=8), and the first leg 15% (n=11). Largest propulsive forces were generated by the first (2.6 mN) and third (3.0 mN) leg. The second leg generated 0.49 mN, whereas the fourth leg generally generated decelerating forces (–1.2 mN). The first and the third leg also contributed to deceleration (–0.46 mN and –1.7 mN). Leg 2 generates solely propulsive forces. The results indicate that during fast escape maneuvers *C. salei* accelerates

primarily by pulling with its muscle driven anterior legs and does not use the hydraulic leg extension of the hind legs. Also, the major support contributed by the fourth leg is due to muscular stabilization.

#### A7.49—Effects of the tail on take-off performance in peafowl (*Pavo cristatus*)

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Abstract not supplied

#### A7.50—Effect of substrate structure on locomotor performance in geckos

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The capacity of geckos to climb up vertical surfaces is exceptional. This is partly due to the generation of adhesive forces between their toepads and the substrate. Moreover, the magnitude of the adhesive force is thought to be proportional to the area of contact between these two surfaces. In this study, we ran geckos on three substrates differing in degree of potential area of contact. We tested whether the structural differences of the substrates affect maximal locomotor performance (i.e. velocity, acceleration, and mass-specific power output) in a predictable way. Nine adult, non-pregnant *Hemidactylus garnoti* were filmed at 250 frames/s while running up a vertical racetrack covered with (1) a smooth, wooden surface, (2) a wire mesh (mesh width 2mm), or (3) a cloth surface. Each individual was run multiple times (at least five) on each substrate. After digitisation, we obtained measures of instantaneous velocity and acceleration. Mass-specific power output was calculated as the product of velocity and the sum of acceleration and gravity. Both (instantaneous) acceleration and mass-specific power output were significantly higher on the smooth surface than on the two other substrates, while the differences in (instantaneous) velocity were non-significant. Moreover, mean speed (i.e. speed the animals attained after their initial burst) did not differ among substrates. We suggest that geckos cannot produce maximal power on the mesh or cloth substrate as they are unable to generate the frictional forces needed to attain high levels of acceleration.