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A8–BIOMECHANICS OF ARBOREAL LOCOMOTION: A TRIBUTE TO JON BARNES

A8.1
Morphological and biomechanical correlates of differences in arboreal locomotor performance and substrate use in *Anolis* lizards

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Caribbean *Anolis* lizards are well known for their spectacular adaptive radiation in habitat use, performance, and limb shape. Whereas some species such as *Anolis sagrei* live mostly on broad substrates, others such as *Anolis valencienni* utilise mostly narrow arboreal substrates. Whereas *A. sagrei* is a much better sprinter on its preferred broad substrate, *A. valencienni* performs relatively well on the narrowest substrates. Here we examine morphological and biomechanical differences in arboreal locomotion between these two species that may underlie these differences in performance. Additionally, we examine differences in spatio-temporal gait characteristics that might help explain the observed differences in speed and surefootedness. While running, *A. sagrei* takes large steps at high frequency. *Anolis valencienni*, on the other hand, typically takes shorter steps on all substrates and keeps the limbs closer to the body during the swing phase. Our morphological analysis shows that the pro- and retractors of both limb pairs are much better developed in *A. sagrei*. However, the insertion of the knee flexors in *A. valencienni* is such that they can generate relatively larger torques. Additionally, we observed that *A. valencienni* has a tendinous link between the pelvis and the lower leg preventing full limb extension during protraction. The presence of this structure presumably results in a more stable locomotion on narrow substrates by preventing lateral displacements of the center of mass, away from the substrate.

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A8.2
Locomotor behavior of a free-ranging gliding mammal (*Cynocephalus variegatus*)

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One of the biggest challenges in comparative biomechanics is to describe the locomotor performance of animals in their natural environment. This is important because measures of performance in the lab might not directly reflect the behavior of free-ranging animals. Furthermore, the subset of behaviors represented in the lab may not be an accurate representation of the full repertoire of behavioral variation. In gliding mammals, the locomotor forces during take off and landing might have significant outcomes for survival, in avoiding predation or injury. However, these forces have not been measured in any free-ranging animal. This study examined the locomotor behavior of free-ranging colugos (*Cynocephalus variegatus*) using custom-designed data-loggers and traditional radio-telemetry. The logger consists of a three-axis accelerometer sampled at 100 Hz and flash memory allowing 75 h of data storage. This new tool allows the simultaneous collection of both behavioral and biomechanical data in the field. Specifically, nightly foraging distance, the timing and duration of glides, and the peak forces associated with take-off and landing events were examined. Animals were active only between sunset and sunrise and moved approximately 0.5 km per night. Glide duration, a proxy for glide length, predicted peak landing force but not peak take-off forces. Longer glides allowed animals to reduce the impact forces associated with landing. This is further evidence that these gliding mammals actively modulate aerodynamic forces during glides. Examining locomotor behavior and the underlying dynamics in the natural environment allows

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insights into the link between biomechanics and the ecology of organisms.

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A8.3
Locomotion in a complex terrain: Effects of plant trichomes on the attachment of the mirid bug *Dicyphus errans*

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Dicyphus errans Wolff (Heteroptera, Miridae, Bryocorinae) lives omnivorously on a wide range of pubescent plants, and preys on a variety of phytophagous arthropods. In contrast to some entomophagous insects, which are impeded or hurt by plant hairs, this bug can elegantly stalk along trichomes using its legs. It has morphological and behavioural adaptations to hairy plant substrates, where higher predation effectiveness and fecundity of the bug, as well as a shorter developmental cycle, have been previously reported. To study the influence of different types of plant leaf surfaces on the locomotion of *D. errans*, bug traction forces on 14 plant species were measured, and adhesion force tests as well as morphometrical analysis of plant trichomes were carried out. The bug traction force ranged from 0.07 mN on *Brassica oleracea* (Brassicaceae) to 1.21 mN on *Plectranthus ambiguus* (Lamiaceae) and *Solanum melongena* (Solanaceae). Bugs performed considerably better on hairy surfaces, where the force depended significantly on both, the trichome length and diameter. The trichome density and aspect ratio did not influence the bug traction force, whereas and adhesive properties of the plant surface significantly negatively correlated with the force.
It is concluded that hairy plants provide more suitable environment for *D. errans* than waxy ones, since they support better the attachment and locomotion of the bug. Trichomes do not act only as a physical barrier for insect attachment, as it was previously reported by other authors. They may also provide suitable interlocking sites for attachment and locomotion of small specialised predatory insects.

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A8.4
Sticky structures: Fibrillar adhesive design in lizards and arthropods

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Typical adhesives are characterized by soft, tacky materials with elastic moduli well below 1 MPa. Many lizards and arthropods possess subdigital adhesive pads composed of β-keratin or chitin, relatively stiff materials (over 1 GPa). These organisms have inspired empirical and modeling work demonstrating that even stiff materials can be effective adhesives if they take on a fibrillar structure. The morphological diversity across these adhesive fibers (called “setae”), both dry (mediated by van der Waals forces) and wet (mediated by tarsal secretions), allows us to test specific hypotheses regarding their function. Mathematical models predict that fibrillar adhesive performance is improved by (1) increased length, allowing greater tolerance to rough substrates and requiring higher strain energy to detach, (2) increased stiffness, allowing higher packing density while avoiding clumping, and (3) smaller tip size (“contact splitting”), increasing adhesive force per real contact area. We test these hypotheses using comparative phylogenetic methods and existing morphological data. Our findings suggest that, rather than “optimizing” fibrillar adhesive systems, natural selection has generated a diverse array of structures, all of which may aid climbing organisms, but to varying degrees. Ancestral material properties of keratin and chitin may create tradeoffs among the modeling predictions while driving the extensive morphological diversity observed across adhesive setae. Future studies need to correlate morphology with performance to determine which fibrillar structures function better than others.

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A8.5
Climbing and adhesion in tree frogs

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Although tree frogs include members of several frog families, they show strong convergent evolution, especially in respect of the structure of the disk-like adhesive pads located on the end of each digit. They adhere to smooth surfaces by wet adhesion, where adhesive force scales directly with pad surface area. Larger frogs thus face a problem, since they will have a larger mass to pad area ratio. Although hylid tree frogs do not have larger toe pads than predicted from isometry, different hylid species have found other ways to provide partial compensation for this problem. Commonly, mass scales at less than snout-vent length cubed, while the adhesive efficiency of toe pads increases with size. In spite of these adaptations, larger frogs adhere less well than smaller ones. This is less disadvantageous than one might expect, however, since larger frogs are too heavy to be supported by most leaves.
Instead, they grasp objects such as twigs, climbing like a human climber. Indeed, there is a positive correlation between adult size and degree of arboreality, in that the largest species are often found high in the canopy, while smaller species are commonly found in shrubs only a metre or so above the ground. This review will also discuss the results of recent experiments investigating the behavioural strategies that frogs use to avoid falling from smooth surfaces. As our results demonstrate, frogs exhibit postures that reduce the chances of

toes peeling off the surface, the normal method of detachment during walking and jumping.

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A8.6
Locomotion and adhesion in arboreal ants

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Interactions with plants have played an essential role for the enormous evolutionary radiation of insects. However, not much is known about biomechanical adaptations that have enabled insects to maneuver in the canopy and locomote on plant surfaces. Insects are small in relation to the diameters of the plant stems on which they climb. Many stems are effectively flat for insects and often retain an intact primary epidermis, which is usually much smoother than bark and can prevent the interlocking of tarsal hairs and claws.
I will present investigations on two arboreal ants which are faced with different biomechanical challenges. First, Weaver ants (*Oecophylla smaragdina*) are attachment specialists capable of generating large adhesive and frictional forces on smooth substrates. When walking upside-down with loads, they compensate torsional moments by adjusting leg position. Running ants control attachment and detachment by varying shear forces. The direction-dependence of attachment leads to different tasks for front and hind legs during vertical climbing. Second, *Crematogaster* (*Decacrema*) ant partners of *Macaranga* trees are specialised climbers on the anti-adhesive, waxy stems of their host plants, where all other insects fail. As adhesive pads can hardly generate any force on this substrate, these ants climb by digging their claw tips into the thin and fragile wax crystal layer. Moreover, the tiny ants avoid falling by morphological and locomotory adaptations reminiscent of larger climbers such as the longer and more spread-out legs and a climbing posture close to the stem.

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A8.7
Directed aerial descent in tropical arboreal arthropods

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Many wingless vertebrates use aerial gliding (directed aerial descent) to avoid predation or to access resources. Until recently, this behavior was unknown in wingless arboreal arthropods. Here I show that worker ants (Hymenoptera: Formicidae) in seven tropical genera use directed aerial descent to return to their home tree trunk during a fall. Field experiments focusing on the common neotropical species *Cephalotes atratus* showed that the behavior is not location-, tree- or colony-specific. In general, smaller workers of *C. atratus*, and smaller species of *Cephalotes*, are better gliders than larger individuals and species (i.e., they regain contact with their associated tree trunk over shorter vertical distances). Falling ants use visual cues to locate tree trunks, and the behavior is strongly influenced by reflectance properties of potential landing substrates; they preferentially direct their descent to bright white targets when given a choice of colors or shades of gray. Directional control during a jump or fall is thought to be an important stage in the evolution of flight. Gliding in a derived, secondarily wingless lineage such as ants is of limited evolutionary relevance. However, ongoing surveys of directed aerial descent behavior show that the behavior occurs in a broad range of wingless arboreal arthropods, including basal hexapods.

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A8.8
Walking and climbing on small branches: Convergent solutions in chameleons, marsupials, and primates

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Many tetrapod vertebrates are able to move on trees so long as the support diameter is large, but only a few groups have developed the specialized adaptations to foraging on small branches. Quadrupeds that climb and walk on such narrow supports face two key problems: controlling the gravity-induced momentum imposed on the body axis (balance) and reducing the gravity-induced forces imposed on the limbs (compliance). The combination of prehensile extremities and simultaneous footfalls of diagonally opposite limbs increases the balancing abilities of primates, arboreal marsupials, and chameleons over those of other arboreal vertebrates by allowing them to shift their weight dynamically sideward, or backward and forward.
Chameleons, arboreal marsupials, and primates use a crouched limb posture, but only chameleons and primates possess relatively elongated limbs, which increase step lengths and contact times, and thus, reduce the peak substrate reaction forces. So, chameleons and primates display a highly compliant gait. Arboreal quadrupedalism does not necessarily demand three-dimensional limb excursions. Cineradiographic analyses show that forelimb abduction generally results from constraints in shoulder morphology. But, because the shoulder morphology differs in chameleons and mammals, each had to find different solutions to overcome these constraints. Chameleons support their parasagittal limb excursions by possessing the most mobile scapulocoracoid among reptiles. In primates, by contrast, the "emancipation" of the arm from the scapula was an important pre-requisite for developing locomotor modes reliant on shoulder joint mobility rather than on scapular excursions.

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A8.9
Adaptation of biomechanics in Australian arboreal varanids

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This paper explores the link between kinematics and ecology for Australian varanids. Twelve kinematic variables were recorded which described gait characteristics, hip height, pelvis and femur movement. The effect of speed and size on each kinematic variable were examined and removed. A combination of both univariate and multivariate analyses were used to compare speed and size-corrected kinematic variables with five ecological traits; retreat site, habitat, openness of habitat, climbing ability and foraging mode. Differences in kinematics were observed between open habitats and closed or semi-open habitats, as well as between climbing and non-climbing species. Species from open habitats had longer stride lengths and step lengths, while species from closed or semi-open habitats had a lower hip height and a greater change in pelvic tilt and yaw. These results were consistent with increased manoeuverability in closed habitats, and increased speed in more open habitats. However, these differences were not significant when analysed in a phylogenetic context, suggesting adaptation of these patterns cannot be confidently inferred.
The greatest differences observed were between climbing and non-climbing species. Climbing species have a lower effective hip height, a shorter stride length and greater forward extension of the femur at footfall. These associations were significant when analysed using both non-phylogenetically corrected and phylogenetically corrected methods. These results were consistent with adaptation to a climbing habitat. Kinematic differences for climbing support biomechanical predictions for increasing stability on narrow or inclined surfaces, while kinematic patterns associated with non-climbing species show associations with speed.

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A8.10
Biomechanical analysis of arboreal locomotion in bonobos: Context, concepts and first results

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The emergence of bipedal locomotion is generally considered a key event in human evolution. One theory proposes that this adaptation occurred in a terrestrial context (i.e., from terrestrial quadrupeds). An alternative theory suggests that arboreal locomotion was preadaptive for hominin bipedality.
One way to explore the power of these theories is to study the locomotor mechanics of extant model species. Bonobos (*Pan paniscus*) have been argued to be suitable in this respect, but quantitative kinesiological arboreal data were lacking. To study kinematics and dynamics of arboreal locomotion in bonobos, an instrumented climbing pole was constructed. This allowed the measurement of 3D-pole reaction forces for single foot or hand contacts at different inclines (0° to 90°) in combination with 3D-kinematics (multiple video-recordings). Spatio-temporal gait characteristics, postural (kinematical) differences and pole-reaction-forces are compared between different inclines as well as with similar data for terrestrial locomotion. The first results suggest that the rates at which spatial aspects of gait change with speed are lower on arboreal inclines compared to those observed for terrestrial and horizontal arboreal locomotion. Yet, on the average, step lengths as such decrease with incline, being largest for quadrupedal horizontal locomotion (terrestrial and arboreal) and smallest at a 90° incline. Bipedal terrestrial steps are even smaller than those at 90°. Temporal aspects of gait change similarly with speed in all conditions. The interaction between incline and posture determines the complex changes of the pole-reaction-forces at hands and feet.

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A8.11
The role of attachment organs in the larval locomotion of the beetle *Gastrophysa viridula*

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Adults of the green dock beetle *Gastrophysa viridula* (Coleoptera, Chrysomelidae) use tarsal adhesive setae to attach to and walk on smooth vertical surfaces and ceiling. In contrast to adults, their larvae apply for a similar purpose two sets of adhesive structures: soft smooth pretarsal pads and a so called rectal organ, located at the posterior end of the abdomen. High speed video recordings at 250 fps were used to analyze the gait pattern of larvae of different instars. The combined use of two attachment systems results in a specific way of locomotion, which is entirely different from that of adults using a tripod gait. Larvae simultaneously swing their contralateral legs, while adhering by the rectal organ, and then swing their abdomen, while adhering by pretarsal adhesive structures. Behavioral observations show that younger instars more rely in their locomotion on the use of the rectal organ, whereas older instars use legs more intensively. Experiments with partial covering of leg attachment organs and the rectal organ by molten wax demonstrated that larvae had difficulties to properly adhere their rectal organs without simultaneous use of adhesive organs of their legs.

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A8.12
Prey capture behavior in *Anolis* lizards: Testing the effect of surface diameter (branches versus flat substratum)

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Feeding strategies in squamates involves a complex series of behavioural activities integrating trophic, appendicular and axial movements. To date, the trophic system and the locomotor design have been studied separately and less often studied in the context of prey–predator relationship. The aim of this paper is to present a first comparative kinematic study of the integration of locomotor and trophic system in the iguanian lizard *Anolis carolinensis* (Iguanidae). *Anolis* lizards are considered as sit- and wait predators using lingual prehension for all kinds of ingested prey, in contrast to the majority of scleroglossan lizards that are often considered as active foragers mainly using jaw prehension. We analyse the predator behaviour in *A. carolinensis* during prey (living crickets) chassing on flat substratum and on narrow branches to measure the potential effect of surface diameter on the kinematic variables of limbs and trophic system during this prey ingestion. A high-speed video system (250 Hz) was used to determine movements of the limbs, the head, the jaws and the tongue for five adult males. Various variables were recorded from analysis of the films (i.e., speed, acceleration, maximal angular movement of the fore and hind limbs, tongue protraction and retraction with the prey). Kinematic curves were built to compare the coordination of movements of the different structural elements under both environmental constraints (flat surface versus narrow branch). Kinematic variables (timing of events and amplitudes) were extracted from curves and compared by using one two-way ANOVA testing the diameter of the surface (fixed effect) and the individuals (random effect) on the integration between locomotor and trophic system.

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