

EDITORIAL



A century of comparative biomechanics: emerging and historical perspectives on an interdisciplinary field

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This Special Issue showcases JEB's central role in historical, current and future comparative biomechanics research. Comparative biomechanics is defined as the scientific study of the mechanics of non-human organisms, including animals, plants and fungi. Mechanics is the branch of physics that addresses the forces and displacements that relate to movement. Comparative biomechanics research is traditionally conducted at the tissue and whole-organism levels, including the mechanical interactions between whole organisms and the environment. JEB's scope is primarily restricted to scientific research on animal systems, yet has included key papers about plants and fungi when the findings have broad relevance to animals. While being an integral part of the newer fields of biophysics (cellular to molecular levels of physics analysis), mechanobiology (transduction of forces at molecular to tissue levels) and bioinspiration/biomimetics (synthetic design based on biological systems), comparative biomechanics enriches ecological and evolutionary biology by integrating mechanics, morphology and the environment through studies across diverse species.

The papers in this Special Issue focus on broad biological questions addressed through the lens of comparative biomechanics. Cross-cutting through time, this Special Issue addresses questions from the vantage points of the history of the field, today's research and the future of comparative biomechanics. Leveraging JEB's range of paper categories, these topics are explored through Commentaries, Reviews and Research Articles. The assembled authors represent diverse contributions – from early career researchers (see associated ECR Spotlight interviews) to senior members of the field. The Special Issue builds from the foundational definition of comparative biomechanics (force and displacement; mechanics) to explore influences of comparative biomechanics on other fields, such as environment/ecology, evolution and engineering.

Biomechanics, by definition, requires measurements and analyses of force and movement. The historical foundation of kinematic measurements and extraordinary advances in the amount and quality of these measurements are captured in McHenry and Hedrick's (2023) Review of imaging technology used across the past century of biomechanics articles. Their analyses of the published literature reveal the correlates of major shifts in imaging technology that have enabled larger datasets and a greater number of sampled individuals. Demuth et al. (2023)

review the remarkable technological advances in 3D reconstruction of morphology and movement, while offering an integrated workflow for researchers wishing to integrate 3D approaches into their studies of organismal movements. Provini et al. (2023) provide a Commentary on the promise and pitfalls of using high-resolution 3D motion data to address questions about complex movement dynamics, and Manafzadeh (2023) offers a Commentary focused on joint mobility with insights arising directly from the major recent strides in 3D imaging and reconstruction.

Focusing on the interface of technology and analyses of animal biomechanics, three papers tackle topics within particular systems – bird bills, cheetah locomotion and hummingbird feeding. Krishnan's (2023) Review of the diverse morphologies, materials, mechanics and sensory capabilities of bird bills exemplifies the powerful discovery space arising from the integration of new technologies – from imaging to materials testing – across one widespread yet diverse animal structure. In Shield et al.'s (2023) Review, the extraordinary capabilities of cheetahs are considered from the lens of technology. By reviewing the historical research about cheetah biomechanics and muscle physiology – many of the discoveries driven by technology – the authors offer insights into sensors and methodologies that apply broadly to other biomechanical systems. The Research Article by Rico-Guevara et al. (2023) uses state-of-the-art high-speed videography and backlighting to understand the active role that hummingbird bills play in helping their tongues transport nectar intraorally, from tongue to throat, shedding light on nectarivory in hummingbirds with extremely diverse bill morphologies.

Technology and biomechanics have also thrived through their alliance with engineering. Harvey et al. (2023) probe the deeply historical and currently burgeoning interface between biomechanics and engineering, specifically from the perspective of flying systems in natural environments. Their Review not only highlights specific areas of translation – related to bird wings – but also offers a synthesis of the deep history of these synergies even beyond the past century and extending to the inventions of Leonardo da Vinci. The engineering–biomechanics connection continues to be an engine of discovery and the rich, data-driven experimental work over JEB's history offers invaluable insights for quantitatively driven engineering translation.

Encapsulating the crucial interconnections of biomechanics and naturally variable environments, Koehl (2023) begins her Review with a quote from Vogel and Wainwright's lab manual 'Structure without function is a corpse, and function without structure is a ghost', and follows with her own twist: 'and an organism without its environment is a mirage'. Koehl's Review examines classic biomechanics topics – from locomotion to biomaterials – and for each example, she highlights the shift in understanding when the role of the environment is included, such as animals carrying cargo or materials adjusting to environmental loads. Clifton et al. (2023) probe a similar theme from a pragmatic position – how can

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researchers systematically yet broadly study animal walking on naturally variable substrates? Taking these themes to the air, Combes et al. (2023), in a Research Article, focus on measuring insect flight in natural environmental conditions. Their study exemplifies how new technology enables massive datasets from which subtle but crucial adjustments by animals in the natural environments are quantitatively addressed.

The integration between biomechanical systems, technological developments and environment–system interactions is exemplified in Nirody (2023) and Jimenez et al.'s (2023) Reviews. Nirody explores exciting new developments emerging from system–environment interactions in a neural framework through studies of panarthropod locomotion. Her Review not only encourages neural–biomechanical integration but also encourages broader taxonomic exploration in biomechanical studies to incorporate deeply historic animals, such as water bears (tardigrades). While Nirody's Review encourages exploration of new systems, Jimenez et al.'s Review encourages revisiting a classic system – fish swimming – via analysis of emergent biomechanical properties of fish bodies in fluids. Like Nirody, Jimenez et al. note the importance of a broad taxonomic incorporation of diverse fishes alongside the use of new technologies to understand system–environmental interactions.

Muscle dynamics is a historical foundation of biomechanics and has been a major focus over JEB's history. Mendoza et al. (2023) review the principles of muscle contractions in the context of diverse animal muscle physiology. The authors connect the historical foundations of force–length and force–velocity relationships to newer discoveries in non-model systems and comparative studies. Their Review encourages engagement of veteran muscle physiologists looking toward new and exciting systems and early career researchers interested in tying together core principles of muscle mechanics. James et al.'s (2023) Review integrates these foundational principles of muscle (and tendon) physiology into the realm of anthropogenic impacts, including endocrine disruptors and climate change. They offer examples of evolved abilities ranging from narrow temperature windows of consistent ability to generate muscle-driven motion, to remarkable toleration of highly variable environments and physiological conditions (such as dehydration). Flash and Zullo (2023) examine muscle physiology and dynamic modeling in the context of muscular hydrostats – mechanisms of long-standing interest to biomechanists given the remarkable capabilities and unusual muscle physiology that enables controlled movements in soft systems. Focusing within this topic of muscular hydrostats, Thompson et al.'s (2023) Research Article examines obliquely striated muscle in squid tentacles that informs a broader understanding of the multiple evolutionary origins of these remarkable muscles.

We hope that readers will explore all the papers in this Special Issue – many not mentioned in this brief, introductory cover article. We hope that this Centenary Special Issue serves as an influential

and enduring reflection on the historical and present-day impact of the field of comparative biomechanics. This collection will hopefully inform wide-ranging communities: early career researchers learning about major historical works and today's relevance, mid-career and senior researchers seeking to enhance their teaching and their own technical skills/perspectives, and funders/scientific administrators who can be provided with these Commentaries, Reviews and Research Articles that exemplify the importance of comparative biomechanics today and into the next century.

References

Clifton, G. T., Stark, A. Y., Li, C. and Gravish, N. T. (2023). The bumpy road ahead: the role of substrate roughness on animal walking and a proposed comparative metric. *J. Exp. Biol.* **226**, jeb245261. doi:10.1242/jeb.245261

Combes, S. A., Gravish, N. and Gagliardi, S. F. (2023). Going against the flow: bumblebees prefer to fly upwind and display more variable kinematics when flying downwind. *J. Exp. Biol.* **226**, jeb245374. doi:10.1242/jeb.245374

Demuth, O. E., Herbst, E., Polet, D., Wiseman, A. L. A. and Hutchinson, J. R. (2023). Modern three-dimensional digital methods for studying locomotor biomechanics in tetrapods. *J. Exp. Biol.* **226**, jeb245132. doi:10.1242/jeb.245132

Flash, T. and Zullo, L. (2023). Biomechanics, motor control and dynamic models of the soft limbs of the octopus and other cephalopods. *J. Exp. Biol.* **226**, jeb245295. doi:10.1242/jeb.245295

Harvey, C., de Croon, G., Taylor, G. K. and Bomphrey, R. J. (2023). Lessons from natural flight for aviation: then, now and tomorrow. *J. Exp. Biol.* **226**, jeb245409. doi:10.1242/jeb.245409

James, R. S., Seebacher, F. and Tallis, J. (2023). Can animals tune tissue mechanics in response to changing environments caused by anthropogenic impacts? *J. Exp. Biol.* **226**, jeb245109. doi:10.1242/jeb.245109

Jimenez, Y. E., Lucas, K. N., Long, J. H. and Tytell, E. D. (2023). Flexibility is a hidden axis of biomechanical diversity in fishes. *J. Exp. Biol.* **226**, jeb245308. doi:10.1242/jeb.245308

Koehl, M. A. R. (2023). Of corpses, ghosts and mirages: biomechanical consequences of morphology depend on the environment. *J. Exp. Biol.* **226**, jeb245442. doi:10.1242/jeb.245442

Krishnan, A. (2023). Biomechanics illuminates form–function relationships in bird bills. *J. Exp. Biol.* **226**, jeb245171. doi:10.1242/jeb.245171

Manafzadeh, A. R. (2023). Joint mobility as a bridge between form and function. *J. Exp. Biol.* **226**, jeb245042. doi:10.1242/jeb.245042

McHenry, M. J. and Hedrick, T. L. (2023). The science and technology of kinematic measurements in a century of the Journal of Experimental Biology. *J. Exp. Biol.* **226**, jeb245147. doi:10.1242/jeb.245147

Mendoza, E., Moen, D. S. and Holt, N. C. (2023). The importance of comparative physiology: mechanisms, diversity, and adaptation in striated muscle. *J. Exp. Biol.* **226**, jeb245158. doi:10.1242/jeb.245158

Nirody, J. A. (2023). Flexible locomotion in complex environments: the influence of species, speed, and sensory feedback on panarthropod interleg coordination. *J. Exp. Biol.* **226**, jeb245111. doi:10.1242/jeb.245111

Provini, P., Camp, A. L. and Crandell, K. E. (2023). Emerging biological insights enabled by high-resolution 3D motion data: promises, perspectives and pitfalls. *J. Exp. Biol.* **226**, jeb245138. doi:10.1242/jeb.245138

Rico-Guevara, A., Hurme, K. J., Rubega, M. A. and Cuban, D. (2023). Nectar feeding beyond the tongue: Hummingbirds drink using phase-shifted bill opening, flexible tongue flaps, and wringing at the tips. *J. Exp. Biol.* **226**, jeb245074. doi:10.1242/jeb.245074

Shield, S. L., Muramatsu, N., Da Silva, Z. and Patel, A. (2023). Chasing the cheetah: how field biomechanics has evolved to keep up with the fastest land animal. *J. Exp. Biol.* **226**, jeb245122. doi:10.1242/jeb.245122

Thompson, J. T., Taylor-Burt, K. R. and Kieret, W. M. (2023). One size does not fit all: diversity of length–force properties of obliquely striated muscles. *J. Exp. Biol.* **226**, jeb244949. doi:10.1242/jeb.244949