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Emerging biological advances enabled by high-resolution 3D motion data: promises, perspectives, and pitfalls

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Abstract

Deconstructing motion to better understand it is a key prerequisite in the field of comparative biomechanics. Since Marey and Muybridge's work, technical constraints have been the largest limitation to motion capture and analysis, which in turn limited what kinds of questions biologists could ask or answer. Throughout the history of our field, conceptual leaps and significant technical advances have generally worked hand in hand. Recently, high-resolution, three-dimensional (3D) motion data has become easier to acquire, providing new opportunities for comparative biomechanics. We describe how adding a third dimension of information has fuelled major paradigm shifts, not only leading to a reinterpretation of long-standing scientific questions but also allowing new questions to be asked. In this paper, we highlight recent work published in and influenced by Journal of Experimental Biology studies, demonstrating the biological breakthroughs made with 3D data. While amazing opportunities emerge from these technical and conceptual advances, high-resolution data often comes with a price. Here, we discuss challenges of 3D data, including low-throughput methodology, costly equipment, low sample sizes, and complex analyses and presentation. We therefore propose guidelines for how and when to pursue 3D high-resolution data. We also suggest research areas that are poised for major new biological advances through emerging 3D data collection.

From two to three dimensions

Our field of comparative biomechanics has grown hand-in-hand with technological advances, allowing for new insights into existing structures, materials, and motions. Central to the study of motion is the need to quantify it, facilitated by modern technical developments across platforms. Arguably one of the most influential advances in modern biomechanics has been the advent and growth of the ability to study organismal kinematics in three dimensions.

Étienne-Jules Marey and Eadweard Muybridge arguably first championed the study of motion with photography (Marey, 1874; Muybridge, 1887) (see Hedrick & Mc Henry in this issue). Both developed imaging techniques that allowed sequential images in rapid succession, acting as the first definable studies of animal gait. Since that time, studies of locomotion with two-dimensional imaging have flourished. The relatively simple recording setup produced a profusion of data from the field and the lab on a variety of animal sizes. Collecting speed data, together with stride and step parameters, for example in vertebrates (e.g., frequency, length, duty factor), clarified the effect of scaling between species (Abourachid, 2001; Biewener, 1982; Biewener, 1983; Biewener, 1990; Blob and Biewener, 2001; Gatesy and Biewener, 1991; McGowan et al., 2008), and within species (Main and Biewener, 2007). The observation and quantification of shifts in gait during avian flight (Spedding, 1986; Tobalske and Dial, 1996), or terrestrial locomotion (Druelle et al., 2021; Hoyt and Taylor, 1981; Maes and Abourachid, 2013; Nauwelaerts et al., 2013; Nyakatura et al., 2008; Schoonaert et al., 2016) provided important insights on the evolution of locomotion (Abourachid et al., 2019; Dial et al., 2015; Hildebrand, 1977). Measuring cranial kinematics of feeding in fishes led to a deeper understanding of the functional morphology (Alexander, 1967, 19; Anker, 1977, 197; Liem, 1967) and hydrodynamics (Muller and Osse, 1978; Van Wassenbergh, 2015; Van Wassenbergh et al., 2006) of this complex system, and also new theories about the evolution and modulation of specialist and generalist feeding behaviours (Liem, 1978; Liem, 1980).

Despite the unquestionable benefits arising from 2D kinematics analyses, applied on an impressive diversity of species and functions, some drawbacks exist. By definition, non-planar motions are impossible to directly quantify using pure 2D recordings. They are particularly frequent in complex, non-cyclical motions, such as grasping or prey capture. Specific set-up tricks can be used to address this problem. One of them could be to limit the motions the studied animal is able to perform to only allow for planar movements (e.g., by building a narrow walking track to only record straight gaits as in Verstappen et al. (2000). The diversity of behaviours that can be captured is therefore limited and their frequent occurrence in natural conditions can be questioned. Usually, 2D analyses tend to focus on whole-body motions, determining the motion of the centre of mass (e.g.,

Nauwelaerts et al., 2015; Nyakatura et al., 2012) or of a geometrical centre, derived from the collected images (e.g., Provini et al., 2012; Provini et al., 2014), whereas relative or independent movements of a specific body part are more difficult to quantify.

Collecting images from more than one view facilitated the first three-dimensional quantifications of motion. Due to technical limitations, views were often taken asynchronously to inform broad-scale motion patterns from multiple perspectives. For example, work exploring the function of the pectoral girdle in flight by Jenkins et al. (1988) combined a dorsal view and a latero-ventral view of a starling flying in a wind tunnel. Thanks to the cyclical nature of the avian wingbeat, the asynchronous data could be interpreted separately and provided a detailed description of complex 3D motions, in this case of the furcula movements during flight. Similarly, the repetitive walking cycle of a quail or the cyclical paddling motions of a ringed-teal, allowed for the reconstruction of a frontal view, built from the temporal synchronisation of the lateral and dorso-ventral views (Abourachid et al., 2011; Provini et al., 2012a). The stereotypic, cyclical, and repetitive nature of locomotor movements perfectly fits these reconstruction methods. Sometimes, the animal accidentally changes its orientation toward the camera during the acquisition. What could be seen as a failure to record a clean movement, happened to be particularly useful. For example, when trying to quantify the oropharyngeal–esophageal cavity (OEC) volume in a white-throated sparrow, spontaneously singing in front of an x-ray camera (Riede and Suthers, 2009), the sudden and unexpected neck rotation, occurring during the production of a similar note, completed the information extracted from the pure lateral view and provided indispensable information to estimate the volume of the OEC.

To obtain synchronous views of the same movement, inclined mirrors were used to split a single view into two. This technique was used with light-based video cameras in a complement of single plane X-ray acquisitions, for example to explore the respiration, eating, and spitting motions of three-spined sticklebacks (*Gasterosteus aculeatus*) (Anker, 1977) or locomotion (Reilly and Delancey, 1997). Early stereophotography, combining two viewpoints, was used to quantify the wake of flying jackdaws (Spedding, 1986), and became a classical method to obtain 3D data (e.g., Ikeya et al., 2022). While capturing multiple views synchronously has become relatively easy overtime, combining those views into 3D information requires a significant effort. Dealing with calibration or distortion can be more challenging, especially out of the laboratory conditions. Yet, these steps are indispensable to fully leverage the potential of 3D data.

Modern computing power now allows us to seamlessly quantify motion in three dimensions, capitalising on two or more views. Systems tracking infrared-reflective markers allowed for rapid

recreation of locomotion in 3D (Pontzer et al., 2009; Warrick and Dial, 1998), while direct linear transformation (DLT) facilitated the reconstruction of 3D motion with two or more camera views (Hedrick, 2008). Since then, open-source versions of these software (see Hedrick, 2008; Jackson et al., 2016; Theriault et al., 2014) have facilitated a burst of new 3D datasets. Additional techniques, including 3D motion capture (see Moeslund et al., 2006 for a summary of methods applied to human motion), silhouette 3D reconstructions (e.g., Fontaine et al., 2009), and 3D temporal scanners that capture motion as a sequence of 3D meshes (Ruescas Nicolau et al., 2022), now also contribute to 3D kinematic datasets.

Journal of Experimental Biology has been leading many of these breakthroughs in 3D kinematic analysis. In 2012, Theriault et al. (2014) reported that 70 papers, or 11% of *Journal of Experimental Biology*'s published content that year, relied on video to measure kinematics. In the most recent full calendar year, 2021, that percentage has increased to 55 papers, or 14% of the publications in the *Journal of Experimental Biology*. Of those, 32 papers, or 8% of total papers, 58% of kinematics-specific papers reported three-dimensional kinematics (See McHenry & Hedrick, this issue, for more details). This paradigm shift in data collection has allowed for either new insights in old questions, which sometimes forced us to update textbooks, or opened questions completely new to science. In the next section, we propose to highlight three case studies, illustrating those scientific processes. In this paper, we are not aiming to provide an exhaustive list of 3D kinematic analyses, but to propose examples, which illustrate the different points of our reflection about what 3D kinematic data can bring to the field of comparative biomechanics.

Case Studies

New Insight: Ventilation and rib complex motions

The mechanics of breathing in crocodilians has been revisited in the light of new observations coming from recent 3D motion visualisation techniques (Brocklehurst et al., 2017). Prior to X-ray reconstruction of moving morphology (XROMM) (Brainerd et al., 2010; Brainerd et al., 2010), two-dimensional fluoroscopy was used to investigate ventilation in crocodilians (Claessens, 2004; Claessens, 2009). While able to quantify the relative contribution of the five mechanisms involved in crocodilian ventilation (e.g., pubic rotation, vertebral flexion, gastral movement, and to a larger extent costal aspiration, and visceral translation)(Claessens, 2009), this method potentially missed fine movements of translations and rotations happening across joints during exhalation/inhalation.

The expansion of the thorax, essential for costal aspiration, is associated with vertebral rib motions powered by intercostal muscles. The morphology of the crocodylian vertebrae, the costovertebral joints – connecting the ribs to the vertebrae – were thought to behave like hinges (Claessens, 2009)(Fig.1).

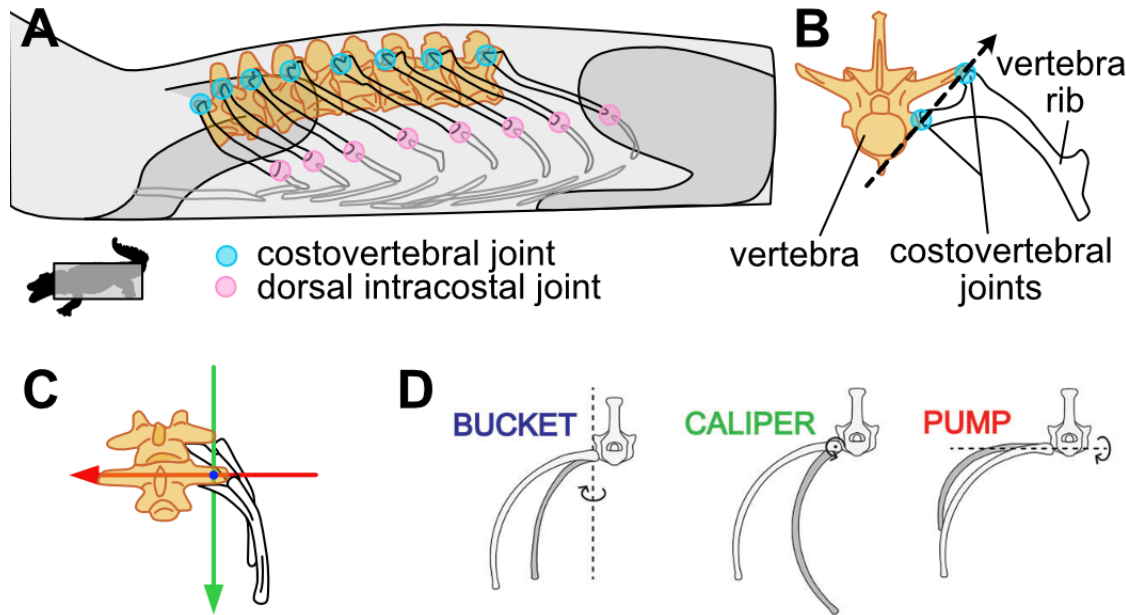


Fig 1. New insights into rib ventilation in archosaurs. A) Anatomical diagram of the ribcage in an American alligator, including the vertebral column (orange), vertebral ribs (black outline), ventral and sternal ribs (grey outline), and costovertebral (blue circles) and dorsal intracostal (pink circles) joints (modified from Brocklehurst et al., 2017). B) The bi-capitate morphology of the costovertebral joint was predicted to constrain this joint to hinge-like motion about a single axis (black dashed line). Figure redrawn from (Hoffstetter and Gasc, 1969). C) Measurements of 3D costovertebral joint kinematics during breathing in live alligators using a joint coordinate system (redrawn from Brocklehurst et al., 2017) D) 3D kinematics showed the functional axis of motion differed from that predicted by the morphology. Specifically, morphological axis underestimates “bucket-handle” motions (blue axis) and overestimates “pump” motions (red axis) (image from Capano et al., 2019).

Contrary to what was previously thought, a detailed 3D kinematics analysis of the costal aspiration of the American alligator (*Alligator mississippiensis*) (Brocklehurst et al., 2017) revealed a high degree of mobility of the intermediate ribs. The authors measured significant rotation about the dorsal intracostal joints with higher magnitude and complexity, especially in more caudal ribs, ruling out the “hinge model” for crocodilians. The axis of rib rotation, previously predicted by joint morphology (Claessens, 2009), appeared substantially different from the functional axis of rotation observed using high-resolution 3D techniques (Fig. 1 C-D). Considering the taxonomic position of crocodilians, generally used as an extant model for primitive archosaurs, this has consequences for the way we reconstruct the evolution of ventilation, one vital function in amniotes.

Updating the textbooks: Tongue motion

The mammalian tongue is a complex muscle and traditionally a textbook example of a biological hydrostat—wherein the tongue is considered “incompressible,” such that shape change in one area causes compensatory shape changes elsewhere (Kier and Smith, 1985). Because the tongue is mostly located inside the buccal cavity during food processing, direct observations are difficult. Historically, the tongue's function during chewing in humans was investigated with subjects who lacked several teeth (Abd-el-Malek, 1955). However, considering the prominent role of the denture during mastication, this method came with limitations. With the increasing availability of fluoroscopy and development of fluoromicrometry (Camp et al., 2016), radio-opaque markers helped to describe and quantify the complex motions (e.g., protraction and retraction) and complex deformation (e.g., changes in thickness) of the mammalian tongue. Over time, the number of lingual markers increased (from 3 to more than 10), together with the frame rate and resolution of x-ray video recordings (Feilich et al., 2021; Olson et al., 2021; Orsbon et al., 2020). The high-resolution 3D data allowed for an accurate description and quantification of the tongue movements, as well as the relative sequence of motions of the jaws and hyoid (Hiemae et al., 1995). Three-dimensional data has changed the way we see the system by adding a new actor - the hyoid - involved in tongue base retraction and the oral phase of swallowing (Orsbon et al., 2020).

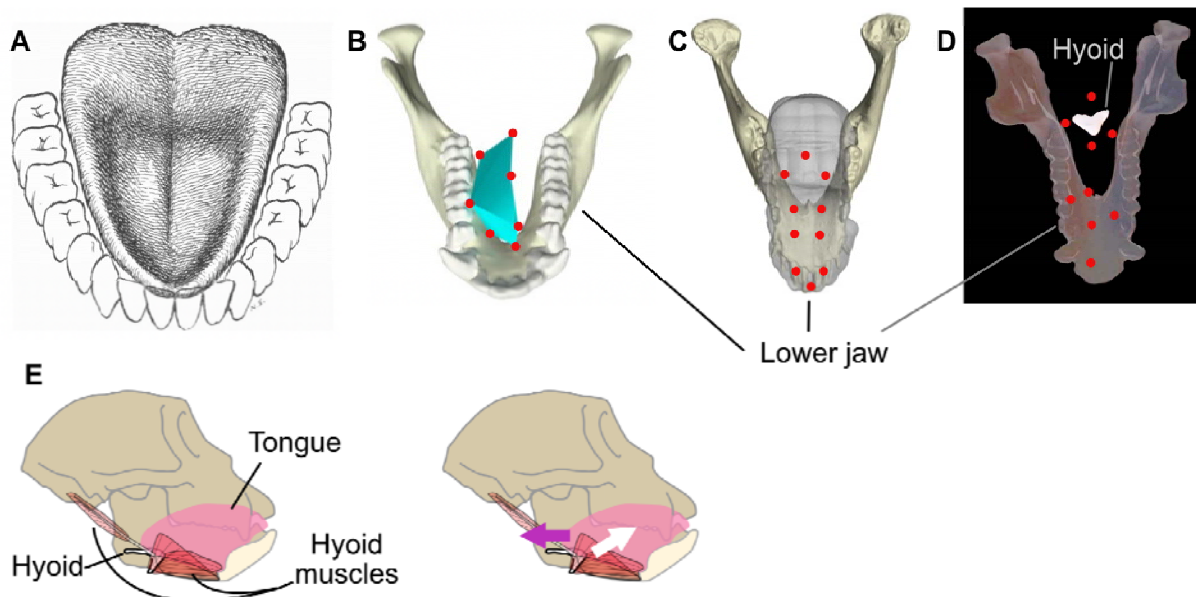


Fig. 2 Improved understanding of the mammalian tongue through 3D kinematic measurements. A) Early observations of tongue shape and deformation were limited to qualitative descriptions in subjects without teeth to obscure the view (image from Abd-el-Malek (1955)). B-D) Biplanar x-ray video and implanted radio-opaque markers allowed researchers to measure 3D, in vivo tongue deformation relative to the jaw (B-C) and hyoid (D) in macaques (*Macaca mulatta*) (B, D) and pigs (*Sus scrofa*) (C). D) These 3D kinematic data have demonstrated the importance of the hyoid apparatus and the muscles acting on it (left figure). As the hyoid moves superiorly and anteriorly (white arrow), the base of the tongue moves posteriorly (magenta arrow) during swallowing in a macaque (right figure). Images modified from Feilich et al. (2021) <https://creativecommons.org/licenses/by/4.0/> (B), Olson et al. (2021)(C), and Orsbon et al. (2020) <https://creativecommons.org/licenses/by/4.0/> (D-E).

Novel Questions: coordinating flight manoeuvres

Motion within the three-dimensional media of air and water has, by virtue of the complexities of the habitat, remained difficult to quantify - early explorations of animals moving in air and water were often limited to laboratory conditions, where motion patterns were kept relatively repeatable and orthogonal to the view. With the advent of accessible 3D tracking, both the media and the organism's motion within it can be quantified, and new work exploring motion within the natural environment has appeared. The resolution we are able to obtain has allowed us to address questions previously unattainable, including questions in the fields of animal behaviour and navigation. Recent examples explored whole-body trajectories during complex behaviours. Two such studies examined collision avoidance in roosting swifts (Parikh et al., 2019), and group behaviour during flocking (Evangelista et al., 2017), by collecting 3D kinematic data in a natural setting. Chimney swifts roost communally, with hundreds of animals flying into a single roost site within a short timescale (Fig. 2). Parikh et al. (2019) discovered that during group landing events, animals coordinate landings by adopting slightly different approach angles and/or by following other

animals closely. Work with this same species also established that birds relied on physical distance to all neighbours during flocking flight (Evangelista et al., 2017). Further work on flocking behaviour in Jackdaws found that these same spacing rules change depending on circumstances - birds flocking in a straight line maintained physical distance between neighbours, but birds flocking during a mobbing event maintain metric distances, which allow flocks to become more ordered as density increases (Ling et al., 2019). Without 3D tracking, the interactions between individual animals would be impossible.

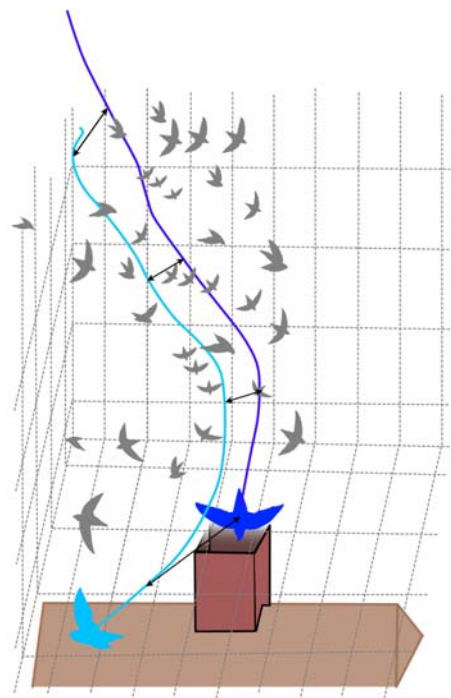


Fig. 3 Reconstructing 3D trajectories of chimney swifts to discover how they coordinate entry into a chimney roosting site. Shown are the trajectories of two birds: one entering the chimney (dark blue line and bird silhouette) and one that did not enter (light blue line and bird silhouette), with the distances between these two birds shown with black arrows. Calculating these 3D trajectories allowed researchers to uncover how individuals interact within a flock. Figure modified from Parikh et al. (2019), bird silhouettes modified from an illustration by Gabriela Palomo-Munoz <https://creativecommons.org/licenses/by-nc/3.0/>.

Potential pitfalls of high-resolution 3D data

The examples above demonstrate the versatility and power of high-resolution 3D kinematics, but this method is not the answer to all questions about organismal motion. Below we highlight four of the main limitations of high-resolution 3D techniques. While we suggest strategies and recent advances to minimise these limitations, there will always be trade-offs. Generally, the detailed depth of high-resolution 3D data comes at the cost of breadth of behaviours, replicates, or species. Before embarking on a study, it is worth considering whether 1) a research question can only be answered

with 3D kinematics and 2) how the limitations will be overcome (Fig. 3). Our goal is to provide a framework for understanding when these methods may be most useful, and when alternative approaches should be pursued.

Lengthy analysis

High-resolution 3D kinematics are rarely a high-throughput method. The rate-limiting step is usually the processing of images to extract 3D measurements, which can include calibration, marker tracking, marker identification, and aligning morphological models to kinematic images. By comparison, collecting the images to analyse is relatively quick. Indeed, modern recording equipment has made it dangerously easy to collect an enormous amount of data from more cameras, with high-resolution images, at high framerates, over larger volumes, with more markers. These large datasets demand substantial time to analyse, and excellent data management to record and link essential metadata throughout the analysis (Brainerd et al., 2017). 3D analysis methods have also improved, e.g., computer-based calibration, tracking software, automated or semi-automated tracking algorithms, but extracting high-resolution 3D kinematics still requires a substantial amount of time and expertise, especially if the highest precision and accuracy is required. This can make 3D kinematic studies expensive in terms of the time, computing power and staff required. We do expect analysis methods will continue to become faster and cheaper, with exciting recent developments including DeepLabCut (Mathis et al., 2018), Autoscooper (Miranda et al., 2011), DANNCE (Dunn et al., 2021). Whether these analysis tools can keep pace with the increasing size of image datasets—or reach the point where most high-resolution 3D kinematics can be a high-throughput method—remains to be seen.

Expensive equipment

Many forms of high-resolution 3D kinematic data collection require large or expensive equipment that limits their accessibility. Some of the most expensive examples are biplanar x-ray videography and video motion capture, which require both specialised equipment (e.g., x-ray machines, multiple high-speed cameras) and specialised environments (e.g., power sources and radiation protection; space to position a large array of cameras). Because of the cost to build and maintain these systems, accessing them as an external user may also be quite expensive. Additionally, such equipment often restricts data collection to artificial, laboratory environments (but see recent work in the field such as Clifton et al. (2015); Combes et al. (2012); Evangelista et al. (2017); Warrick et al. (2016)). Looking forward, we expect the cost of 3D kinematic recording equipment to decrease somewhat and for these data collection systems will become increasingly available. We are also encouraged to see a growing number of cheaper methods being developed to collect 3D

kinematics, such as PiROMM (Falkingham et al., 2022), VROMM (Hoffmann et al., 2018; Jimenez et al., 2018), and smartphone-based 3D motion capture (Aoyagi et al., 2022; Reimer et al., 2022). Many of these take advantage of the fact that cameras with sufficient resolution and frame rate are now less expensive—or already available in a researcher's smartphone. However, there can be trade-offs in the type of data that can be collected (speed, resolution, imaging volume, etc.) and the ease with which it can be analysed. It is worth considering whether a reduction in equipment costs is worth an increase in analysis time.

Low sample size

Because of the time and cost to collect and analyse high-resolution 3D data, these studies are usually limited to low sample sizes. This can be a fatal obstacle for studies that require high statistical power to answer their research question. Studies looking for relatively small effects in relatively variable populations are most vulnerable to these limited sample sizes. It is also difficult to carry out comparative or evolutionary studies that would require high-resolution 3D kinematics from a relatively large number of species. Although as more studies are completed and the data made available, sample sizes and number of species can potentially be increased by “recycling” data from previous studies. As the analysis time and equipment costs decrease, we expect it will be possible to increase sample sizes for high-resolution 3D data -- to some extent (see figure 3 in McHenry & Hedrick, this issue). We do not believe these will become high-throughput methods for analysing hundreds of individuals, although we would be thrilled to be disproved.

Complex analysis and communication

Even once high-resolution 3D kinematics have been collected and analysed from a sufficient sample size, it is not always intuitive how the data should be measured and reported. Compared to 2D motion analysis, 3D motion is by its very nature more complex and more difficult to visualise on 2D screens and pages. While many fields developed standard 2D methods and measurements, there are far less established standards for reporting 3D kinematics, with the exception of human biomechanics (Wu et al., 2002; Wu et al., 2005). As a result, it can be a struggle to make 3D kinematic results clear and reproducible. Very often, 3D kinematics data are recorded to ensure that the studied motion can be correctly projected and further analysed on classic 2D planes (e.g., lateral, frontal planes). The 3D kinematics of a limb or head can be measured in a nearly infinite number of ways, depending on what it is measured relative to, and how the three dimensions are oriented. The challenge is to produce simple and elegant measurements from these complex and often messy datasets.

While 3D motion will always be complex, we are hopeful that improvements in standardisation and visualisation will make these datasets easier to understand and replicate. For example, Gatesy et al. (2022) has proposed standard methods for measuring and reporting 3D posture and kinematics of the hindlimbs of archosaurs and standards for measuring many body regions exist for 3D human kinematics (Wu et al., 2002; Wu et al., 2005). If research communities can create similar standards for other anatomical regions and taxa, this would greatly improve the reproducibility and clarity of 3D kinematic studies. Although we acknowledge that there will always be exceptional structures or organisms that fall outside any set of standards – that is the delight of biological diversity.

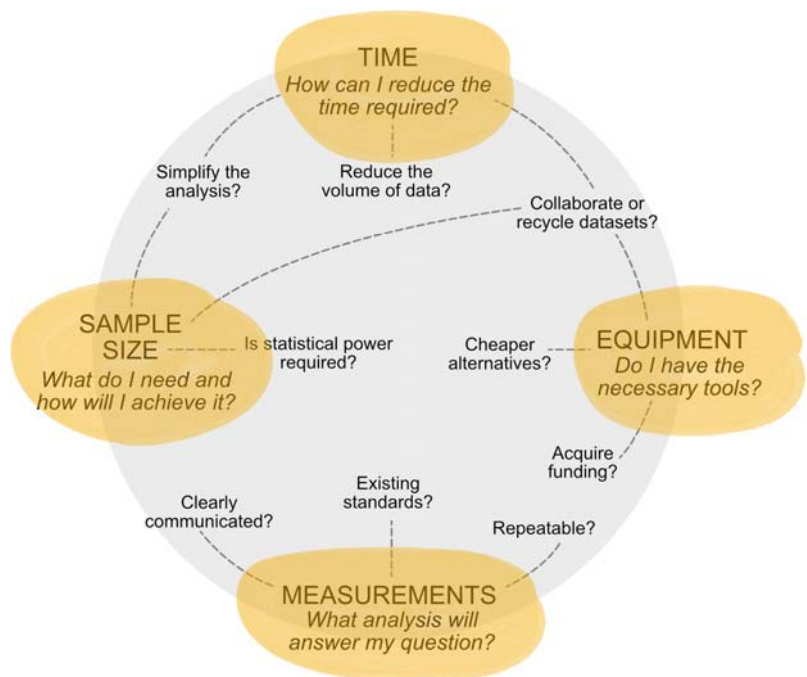


Fig. 3 Guiding questions to minimise pitfalls and maximise best practices methods of high-resolution 3D kinematics studies. For each of the four pitfalls (highlighted in yellow), questions are suggested to guide researchers to identify the most appropriate solution for their study. We envision questions—to consider throughout the research process—to explore how to reduce the impact of these limitations on your study.

Future directions and promises of high-resolution data

Adding a dimension has powerfully shifted our understanding of motion, informed old questions, and added new areas of study to our growing understanding. As technology develops further, new research areas continue to open. Challenging materials, such as the muscle, tendon, skin, and soft tissue, can now be visualised and quantified in 3D. Soft tissue has traditionally been

difficult to study *in vivo*, due to both obstacles in visualisation, and complex shape changes in 3D. Muscle fibres, for example, tend to take on complex shapes and patterns of activation, such that the muscle as a whole may change shape, orientation, and even function in different patterns at different locations within the same muscle. Simplified models using muscle length change as a proxy for force production are likely incorrect (Bishop et al., 2021). By combining 3D studies with x-ray data (Brainerd et al., 2010), magnetomicrometry (Taylor et al., 2021), or ultrasound (Genna et al., 2021) to visualise the underlying muscle shape changes in living animals, we have only scratched the surface of muscle function. Skin, too, changes shape and material properties when in use - a dramatic example being the wing skin of bats, that can change tension during a single wingbeat to alter aerodynamic properties of the airfoil (Cheney et al., 2022).

3D datasets now come from a variety of sources and techniques, from video data to computer rendered 3D models and computer learning. X-ray computed tomography provides detailed visualisation of structures and can even quantify changes in shape and function. The pitcher plant *Nepenthes gracilis* deformation was recently digitised using microtomography, illustrating how the lid deformation in 3D contributed to jerk forces necessary to capture prey (Lenz and Bauer, 2022). 3D models created using stereo imaging correlation (3D-DIC) tracked venus flytrap opening motions, exploring how smooth bending, followed by a snap in some species, reestablishes the open trap (Durak et al., 2022). 3D ultrasound has recently allowed us to explore *in vivo* skeletal muscle contraction (Lopata et al., 2010) and tongue kinematics (Genna et al., 2021).

The combination of detailed, rich datasets with increased digital accessibility enables a single kinematic dataset to have a research longevity well beyond its initial research program, by contributing to further studies. Future access and usage of kinematic datasets beyond the initial study's scope is a growing possibility, thanks to databases of both raw and processed data, increased adoption of open-access policies, and good data management (Brainerd et al., 2017). 'Recycling' existing datasets to examine new research questions facilitates new research areas while avoiding additional protocols, time, and expenses. For example, Evangelista et al. (2017) and Parikh et al. (2019) use the same dataset to address different questions, while the dataset from (Camp et al., 2015) was reused in two new analyses (Camp and Brainerd, 2015; Olsen et al., 2017). While such databases require meticulous associated metadata and open formatting, the potential pay-off is high, and we would encourage future studies to incorporate plans to maximise the longevity, discoverability, and accessibility of their dataset.

Existing studies should be used to address further questions within the organism's functional boundaries, but they can also contribute to wider-scale comparative work (Brainerd et al., 2017). As previously discussed, comparative work in biomechanics has traditionally been difficult due to the time-demanding nature of obtaining the datasets themselves. Often, comparative work was limited

to less than a handful of different species (such as Provini and Abourachid (2018) and Crandell and Tobalske (2015)). However, as more studies are carried out, there is the possibility to combine existing studies to create a comparative dataset with a larger sample of individuals and/or species. This exciting possibility highlights the need for good data management for storing datasets and making them discoverable and accessible to future collaborators. In recent years, this has expanded due to both the readily accessible nature of past datasets and the rapidly advancing automation strategies to digitise kinematic data (such as Clifton et al., 2020; Young et al., 2022; Zhan et al., 2021). We have no doubt that in the coming years, increased automation and accessibility will facilitate detailed comparative work.

Unique kinematic datasets can now be complemented by additional communities of researchers focusing on different types of high-resolution data, including functional morphology databases, phylogenies, ecologies, and genomic data. When combined, these can provide insightful answers to questions about ecology and evolution. Large-scale functional morphology datasets (e.g., Bardua et al., 2021; Brosse et al., 2021; Evans et al., 2021; Ryan N. Felice et al., 2019) are ripe for further kinematic exploration. Combining multiple types of data across disciplines is becoming easier due to the digitization of this data. For example, digital archives join morphological and ecological data across species - AVONET (Tobias et al., 2022) for birds, FISHBASE (Froese and Pauly, 2000) for fish, even Sharkipedia (Mull et al., 2022) for elasmobranchs. More specialised databases, such as XenoCanto for vocalisations in birds and Watkins Marine Mammal Sound Database, exist as well. A natural next step would be to identify groups of interest for future kinematic studies by cross-correlating different existing data types. When combined with detailed phylogenies facilitated by nextgen data (such as Prum et al. (2015)), future comparative studies are well positioned. It is worth highlighting that historical museum collections continue to evolve beyond specimen-based collections to incorporate digital next-generation sequencing and morphological data, which in turn can facilitate rapid digital cross-correlation between data types (Muñoz and Price, 2019). Museums remain crucial to serve as a repository and hub for bringing together different research communities creating new datasets.

Conclusion

We hope that the future of 3D kinematic studies continues to flourish with the advancement of technology and would encourage future research to prioritise both realistic data collection practices as well as incorporate best practices to maximise data longevity: with a focus on repeatability, meticulous metadata, and accessible archiving. With care in planning our data collection techniques, modern 3D data collection and analyses techniques will continue to illuminate the motions around us for years to come.

With the advancement of 3D analysis capabilities, new questions are now testable, allowing us to both update our knowledge and fill in the 'blind spots' in comparative biomechanics: from breathing in crocodilian, to exploring mammalian tongue dynamics, quantifying aerial flight manoeuvres, and well beyond. As 3D motion better represents 'real-world' conditions, it will directly input toward building better understanding of form-function relationships in the field of biomechanics. The reach of these datasets can go beyond our biomechanics niche - with applications to physical, digital, and robotic models with health, industry, and teaching.

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Competing interests

The authors have no competing interests to declare.

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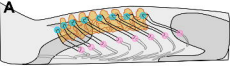
Figure legends

Fig 1. New insights into rib ventilation in archosaurs. A) Anatomical diagram of the ribcage in an American alligator, including the vertebral column (orange), vertebral ribs (black outline), ventral and sternal ribs (grey outline), and costovertebral (blue circles) and dorsal intracostal (pink circles) joints (modified from (Brocklehurst et al., 2017)). B) The bi-captiate morphology of the costovertebral joint was predicted to constrain this joint to hinge-like motion about a single axis (black dashed line). Figure redrawn from (Hoffstetter and Gasc, 1969). C) Measurements of 3D costovertebral joint kinematics during breathing in live alligators using a joint coordinate system (redrawn from (Brocklehurst et al., 2017)) D) 3D kinematics showed the functional axis of motion differed from that predicted by the morphology. Specifically, morphological axis underestimates “bucket-handle” motions (blue axis) and overestimates “pump” motions (red axis) (image from (Capano et al., 2019)).

Fig. 2 Improved understanding of the mammalian tongue through 3D kinematic measurements. A) Early observations of tongue shape and deformation were limited to qualitative descriptions in subjects without teeth to obscure the view (image from Abd-el-Malek (1955)). B-D) Biplanar x-ray video and implanted radio-opaque markers allowed researchers to measure 3D, in vivo tongue deformation relative to the jaw (B-C) and hyoid (D) in macaques (*Macaca mulatta*) (B, D) and pigs (*Sus scrofa*) (C). D) These 3D kinematic data have demonstrated the importance of the hyoid apparatus and the muscles acting on it (left figure). As the hyoid moves superiorly and anteriorly (white arrow), the base of the tongue moves posteriorly (magenta arrow) during swallowing in a macaque (right figure). Images modified from Feilich et al. (2021) <https://creativecommons.org/licenses/by/4.0/> (B), Olson et al. (2021)(C), and Orsbon et al. (2020) <https://creativecommons.org/licenses/by/4.0/> (D-E).

Fig. 3 Reconstructing 3D trajectories of chimney swifts to discover how they coordinate entry into a chimney roosting site. Shown are the trajectories of two birds: one entering the chimney (dark blue line and bird silhouette) and one that did not enter (light blue line and bird silhouette), with the distances between these two birds shown with black arrows. Calculating these 3D trajectories allowed researchers to uncover how individuals interact within a flock. Figure modified from (Parikh et al., 2019), bird silhouettes modified from an illustration by Gabriela Palomo-Munoz <https://creativecommons.org/licenses/by-nc/3.0/>.

Fig. 4 Guiding questions to minimise pitfalls and maximise best practices methods of high-resolution 3D kinematics studies. For each of the four pitfalls (highlighted in yellow), questions are suggested to guide researchers to identify the most appropriate solution for their study. We envision questions—to consider throughout the research process—to explore how to reduce the impact of these limitations on your study.



● costovertebral joint
● dorsal intracostal joint

