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A Novel Multidisciplinary Approach for Reptile Movement and Behavior Analysis

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ABSTRACT

The study of animals’ activity and behavior in the wild is an extremely challenging task. Although tri-axial accelerometers are invaluable for behavioral analyses, their use is more frequent in large charismatic endotherms with limited application in ectotherms. The scarce utilization of this methodology on small-size reptiles is focused on animals’ activity and energetics, showing few records of rapid displays and behavior signals. Here, we present a novel multidisciplinary approach capable of advancing research on reptiles’ behavior. Our proposed approach uses advanced technologies for the digitization, reconstruction and visualization of reptiles and their behavior. We (i) record movement through tri-axial accelerometers, video cameras, and motion capture systems; (ii) ground-truth data through the video records; (iii) develop realistically accurate 3D avatars of the recorded movement for visualization purposes, and (iv) archive data on a Behavior Pattern Database. As case studies, we used two small Mediterranean reptiles, the lizard *Laudakia cypriaca* and the snake *Dolichophis jugularis*. Through our approach, we successfully recorded, ground-truthed, and labeled for the first time, several detailed movements and behaviors of the two case study species. We developed an accurate digital overview of those movements using motion capture and 3D animal reconstruction. Finally, we structured a database for archiving all behavioral data and demonstrated how those archives can be used for advancing behavioral research, providing ecological insights into this animal group. Our approach can enhance research on reptiles’ behavior by contributing to the analysis of complex or isolated behaviors, poorly studied, such as signals and social interactions, providing valuable insights and assisting behavioral analysis.

1 | Introduction

Understanding animal behavior is a fundamental core of biology and an important precondition in wildlife ecology (Morrison et al. 2006; Byrnes et al. 2011) and conservation (Cooke 2008; Manning and Dawkins 2012). Behavioral studies have been carried out on numerous groups of species from invertebrates (Robson et al. 2012) to primates (Erkert and Kappeler 2004; Crofoot et al. 2010). These studies often reveal a wealth of information that cannot be obtained by population-level surveys, including information on fine-scale variation over space and time (Aebischer, Robertson, and Kenward 1993; Aarts et al. 2008) contributing significantly to targeted conservation (Schofield et al. 2007; Hebblewhite and Haydon 2010).

Technological advances have made available many variants of small animal-borne sensors that can enhance the amount of information related to physical or physiological measurements and environmental variables (Wilson, Shepard, and Liebsch 2008; Murchie et al. 2011). Those sensors can effectively improve the study and analysis of animal behavior (Wilmers et al. 2015; Whitford and Klimley 2019). One of those sensors is the tri-axial accelerometer, which can measure the acceleration of an object in three orthogonal axes (*X*, *Y*, and *Z*) (Shepard et al. 2010). The combination of gravitational (due to gravity) and inertial (due to animal movement) acceleration imposed on the device can provide information on the animal's posture and movements (Wilson et al. 2006; Wilson, Shepard, and Liebsch 2008). This information can be used to identify a wide range of behavior patterns (Laich et al. 2008; Shepard et al. 2010) or as a proxy to estimate energy expenditure during movement (Wilson et al. 2006; Wilson, Shepard, and Liebsch 2008; Halsey et al. 2009a). These properties, when combined with other sensors on tagged animals can, in turn, provide insight into individual and population-level processes (Erkert and Kappeler 2004; Gilly et al. 2012), or spatial patterns and habitat usage (Kays et al. 2011; Wilson, Quintana, and Hobson 2012), which may influence the effectiveness of conservation practices.

In recent years, accelerometry has rapidly expanded to cover a broad range of species, with the vast majority of these being large, charismatic endotherms, such as mammals and birds (Allan et al. 2019; Chung, Lee, and Lee 2021; Garde et al. 2022). Among them are several domestic animals (Gerencsér et al. 2013; Smit et al. 2023) and livestock (Riaboff et al. 2022; Jiang et al. 2023). In ectotherms, however, the application of accelerometry is scarce and has focused mainly on measuring the activity of large-bodied snakes, crocodiles (Franklin et al. 2009; DeSantis et al. 2020; Whitney et al. 2021), sea turtles (Halsey et al. 2011; Bidder, Qasem, and Wilson 2012a; Bidder et al. 2012b), and sea snakes (Gleiss et al. 2011; Udyawer et al. 2017). Research on small terrestrial species such as lizards and toads is limited and has focused mostly on recording animals' activity using low sampling rates (1–10 Hz) (Zena et al. 2020; Spiessberger et al. 2023). Distinctive behaviors, such as feeding, digging, walking, and striking, have been identified only for slow-moving tortoises (Lagarde et al. 2008) and large-size rattlesnakes (Hanscom et al. 2023).

Despite reptiles being considered good models for behavioral studies due to their signaling repertoires (Fleishman 1992; Radder et al. 2006; Ramos and Peters 2016), accelerometers have not yet been used successfully within this group for behavioral research. The absence of such kind of tools in behavioral studies could be associated mainly with weight limitations, as the current battery sizes generally preclude accelerometry studies of the smallest (< 100 g) terrestrial animals and birds (Brown et al. 2013; Hammond et al. 2016; Bäckman et al. 2017).

In parallel to recording animal movements, visualization of recorded output is of equal importance in enabling a more comprehensive understanding of animals' behavior. In that regard, 3D photogrammetry and motion capture (MoCap) are providing new opportunities. 3D digital photogrammetry has provided a mechanism for generating intricate digital models of diverse objects (Dixit et al. 2019; Ramos et al. 2022), including living creatures of various sizes, from small frogs to large great whales (Irschick et al. 2020, 2022; Brown 2022). MoCap, with its ability to capture movements and behaviors with lifelike authenticity (e.g., Stavrakis et al. 2012; Mathis et al. 2020), has been used for recording imperceptible movements of animals (Roy et al. 2011; Marshall et al. 2021) including small reptilian creatures (Kwon, Kim, and Lee 2018; Zong et al. 2018). Together, 3D photogrammetry and MoCap can produce accurate digital avatars, which presents an opportunity for accurate reconstruction of animal motion to animal shape (Zotos et al. 2022). These avatars can significantly assist in understanding and representing the complex diversity of movement and behavior.

In this paper, we aimed at:

a. recording distinct rapid movements and behaviors from small Mediterranean reptiles (a snake, *Dolichophis jugularis*, and a lizard, *Laudakia cypriaca*), with tri-axial accelerometers;

b. introducing a novel multidisciplinary approach able to significantly assist behavioral research by combining inputs from (i) tri-axial accelerometers, (ii) visual recordings, and (iii) 3D motion capture;

c. demonstrating the effectiveness of this approach and its contribution to aspects of behavior analysis and visualization.

All behavioral data are archived on a Behavioral Pattern Database while the recorded movements can be projected on realistically accurate virtual avatars of the animals (Figure 1). Although the approach herein is tested on terrestrial reptiles, it can be easily replicated in other species for which direct behavioral observation is challenging, providing valuable insights assisting behavioral analysis.

2 | Materials and Methods

2.1 | Case Studies

In our experiments, we used a starred agama lizard (*Laudakia cypriaca*; sex: M, SVL: 10.7 cm, total length: 19.4 cm, mass: 78 g) and a large whip snake (*Dolichophis jugularis*; sex: M, SVL: 146.0 cm, total length: 189.0 cm, mass: 479 g) from the island of Cyprus, as case studies, for testing the capability of our approach to enabling behavioral recognition and analysis. Both species are widespread on the island. The starred agama is a medium-sized rock-dwelling lizard of the family Agamidea, endemic to Cyprus

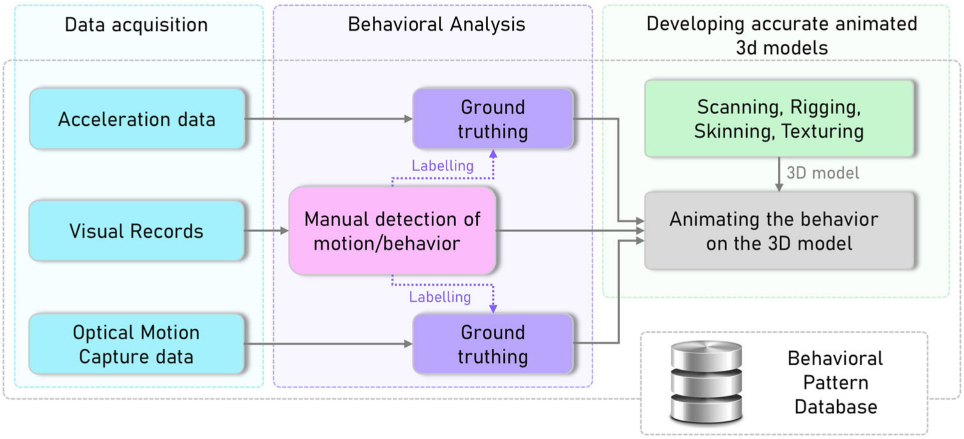

FIGURE 1 | Schematic diagram of the proposed multidisciplinary approach. Three main pillars and several interconnected steps combine their results for the development of the Behavioral Pattern Database (BPD). The archive of the BPD includes motions and behavioral patterns promoting research on selected species as well as visual information assisting visualization.

with a body length of no more than 30 cm. The large whip snake has a thick, muscular, agile body and is probably the longest snake in Europe with lengths up to 3 m (Zotos, Stamatiou, and Vogiatzakis 2023).

The two individuals were collected from the field (*L. cypriaca*: Parekklisia village, latitude 34.776157°N, longitude 33.173852°E, elevation 206 m; *D. jugularis*: Kolossi village, latitude 34.664477°N, longitude 32.937725°E, elevation 40 m) using time-survey during spring 2019 and were released back in the field after the end of the behavioral trials. In all cases, handling and human interaction were kept as limited as possible to minimize stress to the animals. All appropriate licenses had been acquired from the Department of Environment (DE 140/4/19) and Cyprus Bioethics Committee (EEBK 21.1.01.03) prior to collection.

2.2 | Recording Arenas

We recorded the animals' movements in the facilities of the Graphics & Extended Reality Lab at the University of Cyprus, and in the field (Figure 2). Facilities' recordings (May–June 2019) were conducted in two wooden enclosures (2.5 m × 3 m for snake and 1.5 m × 1.5 m for lizard), allowing the free and unobstructed movement of the reptiles in the available space. The enclosures were open from above to allow a direct view of the animals' movement by a set of surrounding cameras. A total of 20 recording efforts (eight for the lizard and 12 for the snake), approximately 10 min each, took place over a period of 4 days to minimize stress to the animals. During recording, animals were left alone to move freely, thus capturing general movements, while in some cases they were induced to climb, strike, flee, or jump as a means to record more specific movements.

Field recordings (July 2019) were made in a semi-natural environment, developed at an agricultural field near Kolossi village, Limassol district (latitude 34.664651°N, longitude 32.937242°E, elevation 40 m). The use of this semi-natural environment maximized the range of behaviors expressed and allowed the acquisition of more complex movements. Two enclosures (10 m × 15 m each) were constructed, and several microhabitats were created in each enclosure including rock piles, haystacks, shaders, and ponds (Figure 2). For the development of these semi-natural structures, we used materials sourced from adjacent agricultural fields, including rocks, hay, logs, and wooden pallets. A plastic membrane was utilized to temporarily retain water in small ponds. The constructed structures were designed to resemble similar existing formations commonly used by the aforementioned species in both the natural and anthropogenic environments of this agricultural area. Prior to the initiation of the monitoring, animals were left to freely explore the enclosures for 1 week as an acclimatization period (Scheun, Greeff, and Ganswindt 2018; Spain, Fuller, and Allard 2020). After that period, animals were continuously monitored and their movements were recorded for 3 consecutive days from early morning (7 a.m.) until late afternoon (7 p.m.).

2.3 | Data Acquisition

Data acquisition on animal movement was achieved via three different complementary approaches: (i) accelerometers, for acquiring high-resolution quantitative data on animal movement, (ii) digital cameras for reference patenting, and (iii) optical motion capture for 3D digitalization and reconstruction. Since each approach was running independently, all data were synchronized manually, to the nearest second. Examples of synchronized views from all methods can be seen in Supporting Information S1–S3.

2.3.1 | Accelerometers

Small-size, animal-borne, tri-axial accelerometers (AXY-4 of Technosmat, weight approximately 3 g) were externally attached to the animals' dorsal area. Following bioethics rules (Soulsbury et al. 2020), the mass of the attached device was less than 5% of the animal's body mass. The position of placement was carefully selected to allow the device to record even the smallest body movement, allowing unobstructed behavior (Wilson and McMahon 2006; Blomquist and Hunter 2007). Accelerometers

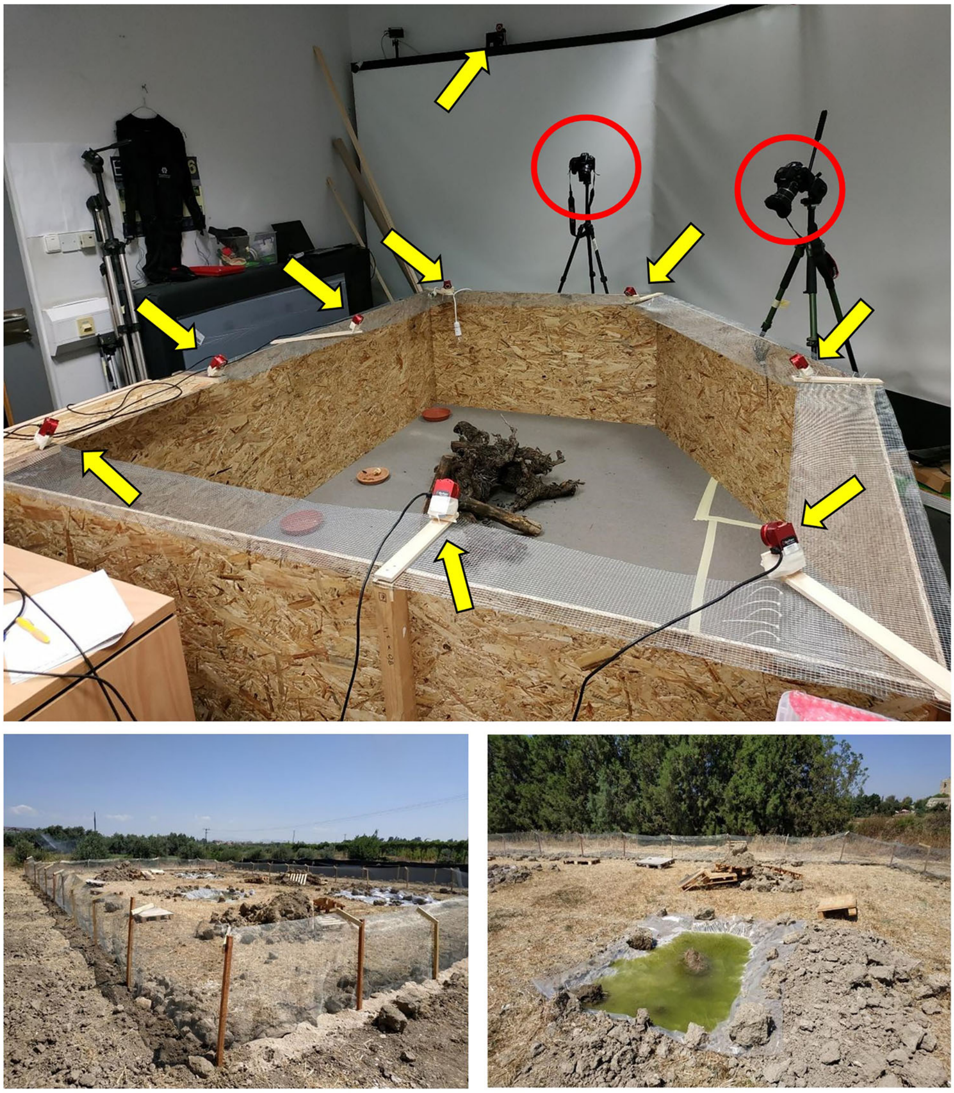

FIGURE 2 | Above: Facilities' enclosure (2.5 m × 3 m) surrounded by 12 Optitrack cameras (yellow arrows) and 4 digital cameras (red circles). Not all cameras are included in the picture. The enclosure was developed in the facilities of the Graphics & Extended Reality Lab of the University of Cyprus. Below left: Field enclosure created to maximize the range of behaviors expressed by the two case study species. The field enclosure was monitored by two digital cameras with zoom lenses. Below right: Detailed view of the microhabitats (e.g., piles, ponds, and busking sites) created within the field enclosure.

were glued in the dorsal area near the neck of the two species (Figures 3 and 4) using non-epoxy glue (Bostik smart adhesive). This rigid attachment ensures the absence of shifts between the tag and the position of the animal, which could affect the interpretation of the tri-axial data (Brown et al. 2013; Shepard et al. 2008). Accelerometers were configured to a sample rate of 100 Hz, a sensitivity of ±2 g, and a resolution of 8 bits. A high recording rate (100 Hz instead of 20 or 40 Hz) allowed us to capture rapid movements such as social interaction and rapid signal displays. High sensitivity (±2 g) increases the resolution of acceleration measurements (from 0.125 g at ±16 g to 0.0156 g at ±2 g) allowing us to record even the slightest movement that might not be adequately recorded at a low sensitivity (Lagarde et al. 2008; Barbuti et al. 2016). Before attachment to the animals, the accelerometers were calibrated to the three-axis (see details on calibration processes in Shepard et al. 2010; Williams et al. 2017).

2.3.2 | Digital Cameras

Different sets of digital cameras were used for the facilities and the field recordings depending on the different needs of each environment. Facilities: One fixed top view (GoPro HERO 7), two fixed site views (Canon EOS 60D and Canon EOS 7D Mark II) and one movable hand camera (Canon PowerShot SX40 HS) were used. All cameras were recording at 24–30 fps with a resolution of 1920 × 1080. Field: Two movable cameras (Canon EOS 60D and Canon EOS 7D Mark II) on stabilizer tripods equipped with zoom lenses (Canon EF 100–400 mm).

2.3.3 | Optical Motion Capture

A passive optical motion capture (MoCap) system with 12 Optitrack Flex 3 cameras (resolution 640×480) was used for capturing

FIGURE 3 | Left: An individual of the lizard *Laudakia cypriaca*, bearing an AXY-4 accelerometer on the dorsal area near the neck and reflectance markers (3 mm) in articulate parts of the body. Right: An individual of the snake *Dolichophis jugularis*, with reflectance markers (14 mm) attached to its body and the detailed placement measurement on the right side.

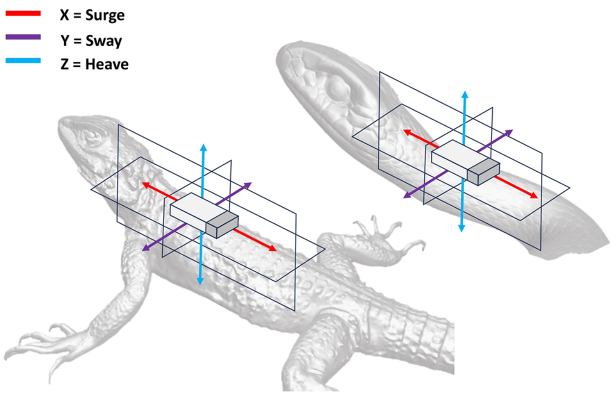

FIGURE 4 | A schematic of the lizard *Laudakia cypriaca* and the snake *Dolichophis jugularis* with a tri-axial accelerometer (gray block) attached to the dorsal area near the neck. Colored arrows on the *X*, *Y*, and *Z* planes show the device axes/orientation of the animal. *X* = surge (red), *Y* = heave (blue), and *Z* = sway (purple). The darker area on the accelerometer indicates the site where the communication pins are situated.

the 3D movement of the animals in the facilities. The system uses markers that are coated with a retroreflective material to reflect light that is generated near the camera's lens. Note that these markers are firmly attached using a non-epoxy glue (3 M Vetbond Tissue Adhesive) at strategic points on the reptile's body (at least one at each limb segment, the head, body, and tail; see Figure 3 and Supporting Information S4). For the lizard, we used a total of 17 small-sized markers (3 mm diameter), while for the snake, we used 12 medium-sized markers (14 mm diameter). The cameras operated at high frequencies (100 Hz), capturing the position of any number of reflective markers within their visual field. Before motion capturing, we calibrated the cameras, obtained their positions, and measured the lens distortion of each camera. Calibration results indicated a millimeter accuracy in the reflective markers' position. The markers were tracked over time and used to reconstruct a complete three-dimensional movement of the reptile's body.

2.4 | Data Processing and Analysis

2.4.1 | Detecting Movements and Behaviors

Data from digital cameras were processed and synchronized using Adobe Premiere Pro (Adobe Inc.). Researchers experienced in reptile behavior (SZ, MS, and SZM) observed the final visual material to detect all movements and behaviors recorded. Whenever an intriguing movement was observed, manual timestamping was employed, and movement was labeled and extracted in .mp4 format for ground-truthing.

2.4.2 | Data Preparation

Acceleration data were extracted into .csv format upon animals' recapture. RStudio (RStudio Team 2020) was used to restructure and convert to an appropriate column formatting to be imported into DDMT software (Daily Diary Multiple trace; WildByte Technologies, Swansea University, Swansea, UK). The date and time were synchronized to the manual timestamping.

Motion capture records were processed using the Optitrack Motive software (https://optitrack.com/software/motive/). Markers were labeled, and motion data were cleaned up, filling in missing information, to ensure tracking accuracy. The labeled markers were thereafter exported in .c3d format, a format that can store 3D coordinate information.

2.4.3 | Ground-Truthing

Distinctive movements were identified via reference patenting (ground-truthing), a method involving the labor-intensive manual assignment of accelerometer waveforms to behavior categories and unique movements (Halsey et al. 2009b; Shepard et al. 2009). This ground-truthing phase was significantly aided by the timestamping approach utilized to synchronize the three independent motion-recording methods (see Section 2.3).

2.4.4 | Behavioral Analysis

The ground-truthed accelerations were used as the matrix for identifying and bookmarking similar movements and behaviors within the acceleration data. The "*Behavioral builder*" and "*Time series*" features of DDMT were used for setting the search criteria on the acceleration channels, their derivatives (pitch, roll, heading), and their differential channels (Wilson et al. 2018). The "*Bookmark multisession*" feature was used for exporting acceleration imprints of bookmarked behaviors in .csv format. Visualization of acceleration and further analysis was performed in RStudio (RStudio Team 2020) using R (R Core Team 2021). For more technical details on the use of DDMT and the features within, and behavioral analysis, see Wilson, Shepard, and Liebsch (2008) and Shepart et al. (2010)

2.4.5 | Animating 3D Visualization

To incorporate recorded MoCap into virtual 3D models of the case study species, we followed a systematic procedure allowing us to match the movements of markers during ground-truthing to the corresponding 3D reptile's model. This procedure aimed at offering an extended and detailed visualization of behaviors though animated models, enabling the observation and enhanced comprehension of animal movements.

This procedure consists of several successive stages including: (i) 3D scanning of a live animal using the Beastcam technology (Bot and Irschick 2019; Irschick, Briggs, and Smart 2019), (ii) 3D reconstruction of the animal body (mesh) through COLMAP software package (https://github.com/colmap/colmap), (iii) replicate the animal's coloration and surface characteristics (2D color texture maps), though MeshLab software (Cignoni et al. 2008), (iv) develop the internal skeleton (control rig) of each animal in Blender (https://www.blender.org), allowing for the manipulation and animation of the animal's 3D model, and (v) integrate the ground-truthed movement of the animal's markers as recorded by MoCap, into the 3D model's control rig (bake animation), using Autodesk MotionBuilder (https://www.autodesk.com), providing animation to the 3D model. Figure 5 illustrates the key steps during this developmental process. For more technical details of this procedure, including information regarding dimensional accuracy, and animating processes see Irschick et al. (2020, 2022) and Zotos et al. (2022).

2.5 | Structuring Behavior Pattern Database

All movement and behavioral information extracted through the above steps were meticulously stored within a Behavior Pattern Database (BPD) developed for this purpose. This database, currently managed using Access software, was designed to ensure easy accessibility for subsequent analyses and to facilitate replication by behavioral researchers worldwide. Figure 6 offers a visual representation of the foundational structure of this repository.

3 | Results

3.1 | Identified Movements

A total of six movements (i.e., walking, running, climbing, jumping, signaling, and body turn) were identified for the lizard *L. cypriaca* and six movements (i.e., slithering, aggressive interaction, climbing, body motions, head turn, and body turn) for the snake *D. jugularis* (Table 1; Figure 7). Small variations of each movement (e.g., slow vs. fast slithering) were also classified. In total, 255 observations were used as reference patenting for *L. cypriaca* (obj. per movement: average = 12.1; min = 1; max = 32) and 379 *for D. jugularis* (average = 15.2; min = 3; max = 35). Time series plots of 100 Hz tri-axial acceleration from indicative movements can be seen in Figure 8. Despite each movement being unique, the acceleration pattern is clearly similar (Figure 9).

For visualization purposes, visual and MoCap data from 10 different movements from each species were selected for imparting motion onto the developed high-quality, virtual 3D models of our two case study species. Those motions were uploaded to a publicly accessible repository of high-quality animated 3D virtual models (http://3dreptiles.cs.ucy.ac.cy) setting the point-of-reference for a digital 3D archive of detailed reptiles' behavior. The use of virtual animals to visualize motion and behavior, despite the obvious difficulties and limitations, encapsulates various advantages over virtual archives of images or videos. (e.g., environmental education) described in detail by Zotos et al. (2022). A simple comparison between movements as recorded via digital cameras and the corresponding movements of the virtual animals is available in Supporting Information S5–S7.

3.2 | Behavioral Pattern Database

The complete set of recorded data (i.e., behavior, acceleration, digital camera, MoCap) related to the examined behaviors along with several metadata (i.e., general species information, detailed individual information, field/area where movements were recorded, name of project if applied, 3D models of the recorded animal, 3D animations of the recorded movement, and details on acceleration device used and adhesive procedure) were successfully archived in the BPD developed for this purpose. The structure of BPD provides various visualization possibilities of behavior in reference including short videos (2–5 s), high-rate MoCap records, and realistic 3D animated models. A complete scheme of the database can be seen in Figure 10. Access to the BPD can be provided upon request.

3.3 | Enhancing Behavioral Research

The usability of our method in behavioral research is demonstrated here using two commonly identified movements (slithering for the snake and running for the lizard) and two distinct behaviors/signals (striking for the snake and head-bobbing for the lizard). The bookmarked criteria of those movements, in the form of DDMT "expression builder" and "time series" files, were retrieved from the PBD, and tested on a RAW 1-h data sample also extracted from the PBD (*L. cypriaca*: 1/8/2019, 09:00 a.m. – 10:00 a.m.; *D. jugularis*: 30/7/2019, 09:00 a.m. – 10:00 a.m.).

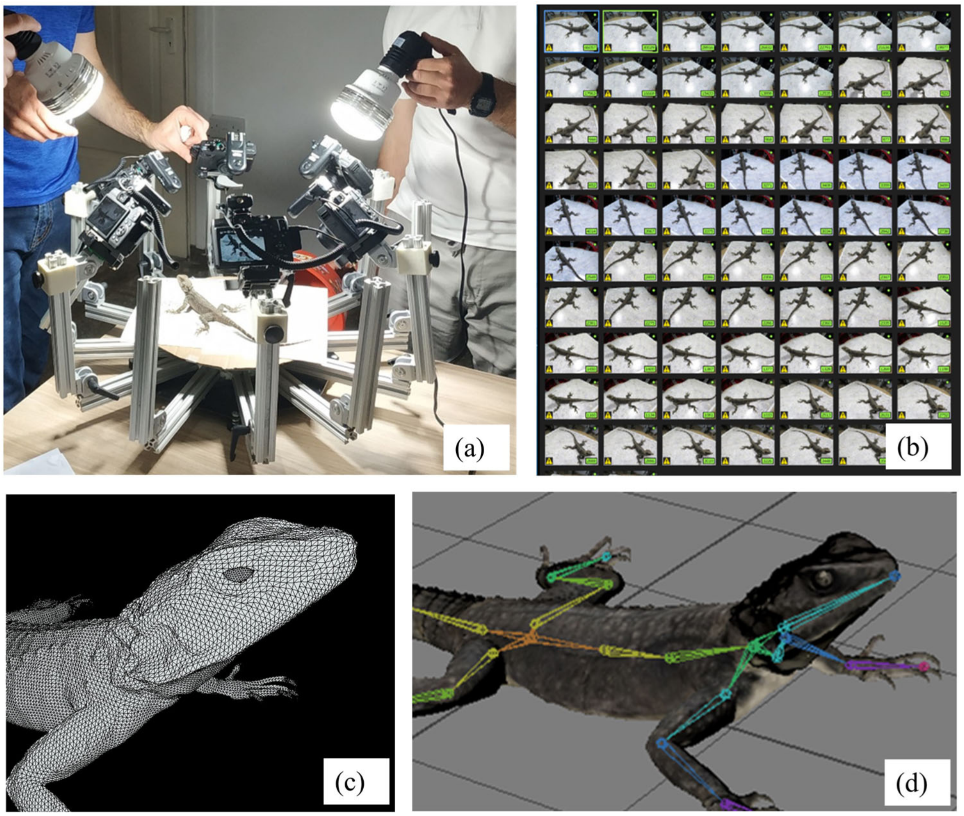

FIGURE 5 | Main steps during the production of 3D animated models. (a) Lizard *Laudakia cypriaca* surrounded by rotating multiple grids bearing cameras that were used for scanning using photogrammetry. (b) Initial scanning results (photos) of the animal taken practically simultaneously from various angles. (c) 3D polygon mesh of the lizard after rendering by the graphic designer using MeshLab. (d) Final 3D model with visible texture (body coloration) and internal rig (virtual bones that allow the model to move).

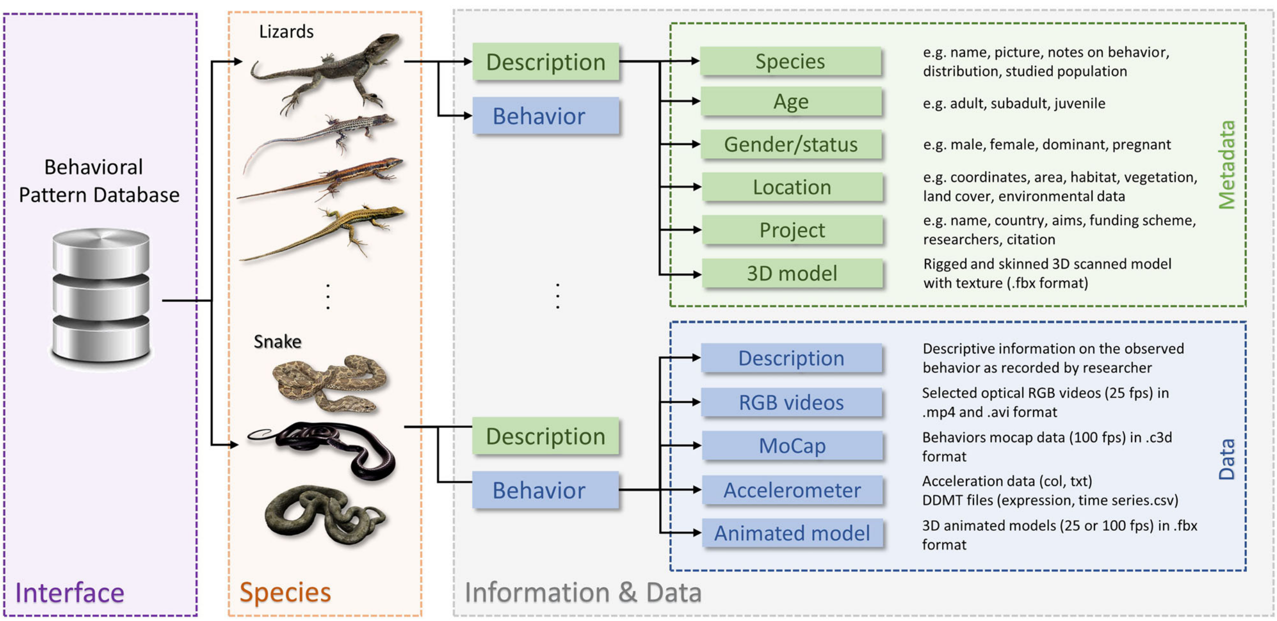

FIGURE 6 | Basic structure of this Behavioral Pattern Database showing the groups of information that have been included and can be extracted upon request.

TABLE 1 | Descriptive information on the movements and their variation recorded during behavioral trials for lizard species *Laudakia cypriaca* and snake species *Dolichophis jugularis*. Movements were recorded through tri-axial accelerometers, digital cameras, and MoCap.

Movement	Variation	Description
Laudakia cypriaca		
Walking	Normal	Moving forward at an average normal speed for the species
	Upwards	Moving upward in a gradient surface (slope) at an average normal speed for the species
	Downwards	Moving downward in a gradient surface (slope) at an average normal speed for the species
	Stop–walk–stop	Bursts of walking or running with sudden stops between them
Running	Running	Rapidly moving forward
Climbing	Up	Climbing a vertical surface
	Down	Descending from a vertical surface
Jumping	Up	Jump from a lower to a higher place (e.g., from the ground to a woodpile or wall/fence)
	Down	Jump from a higher to a lower place (e.g., to descent from a woodpile or wall/fence to the ground)
	Small up	Jump to climb on a small object (e.g., log or rock)
	Small down	Jump to descent from a small object (e.g., log or rock)
Signaling	Head-bobbing (up to down)	Characteristic motion of the head and upper body rapidly moving up to down once or multiple times
	Head-bobbing (down to up)	Characteristic motion of the head and upper body rapidly moving down to up once or multiple times
Body turn	Left	Turn the body by approximately 90° to the left
	Right	Turn the body by approximately 90° to the right
	Right 180	Make an approximately 180° turn of the body towards the right
Dolichophis jugularis		
Slithering	Slow	Slow move of the body forward. Head sways right and left.
	Fast	Rapid move of the body forward. Head sways right and left.
	Surge forward	Slow move of the front part of the body forward without head sways
	On water	Move of the body forward on water. Head sways right and left.
Aggressive interaction	Striking	Sudden ejection/strike of the head and front body part forward to attack
	Defending	Sudden retraction of the head and front body backward
Climbing	Wall (effort)	Effort to climb a straight wall (only by the front part of the body) accompanied by dissenting or collapsing of the body smoothly
	Surface	Moving the body upward and climbing on a surface (i.e., pallet)
Body motions	Front shift	Shifting the head and front part of the body toward right or left. The rest of the body remains stable
	Body elevation	Elevating/lifting the front part of the body in the air as if to look from higher ground
	Searching	Small movements forward/backward, right and left turn of the head, concurrent with the extraction of the tongue as of searching the surrounding environment
	Overpass obstacle	Moving the body upward and then downward to overpass a small obstacle (i.e., log)
Head turn	Head turn 90	Turning of the head by approximately 90° toward the right or left
	Head turn 180	Turning of the head by approximately 180° toward the right or left
	Head up/down	Raising the head up a few centimeters from the ground and dissenting down

(Continues)

TABLE 1 | (Continued)

Movement	Variation	Description
Body turn	Body turn 90	Turning of the front part of the body (sway and yaw) by approximately 90° toward right or left
	Body turn 180	Turning of the front part of the body (sway and yaw) by approximately 180° toward right or left

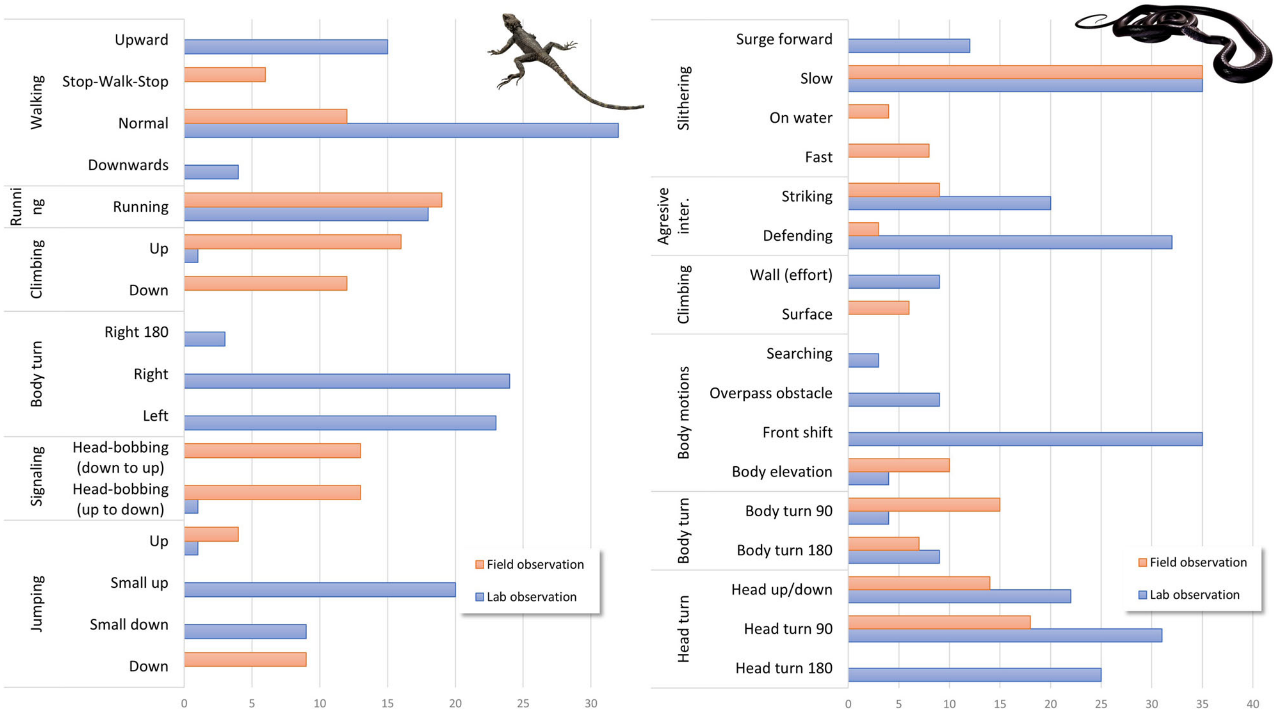

FIGURE 7 | Type of identified behaviors and number of corresponding lab and field observation records for the lizard species *Laudakia cypriaca* (left) and snake species *Dolichophis jugularis* (right).

The RAW data samples were selected to include at least one visual verification of the examined behaviors to be used as a reference. When tested, the bookmarked criteria successfully identified all referenced movements. Manual inspection of the identified events was conducted, and false positives were removed. Summary statistics of the retrieved movements on RAW data samples can be seen in Table 2 while the results of the temporal movement analysis can be found in Figure 11.

For the case of *L. cypriaca* we see that, although head-bobbing signaling takes less than a second, it is a behavior repeated several times within an hour consuming a relatively large amount of the animal's activity level (VeDBA/s). More than 85% of the identified head-bobbing events are conducted in bouts of two to three with an approximate 1-s gap between. If we consider head-bobbing not as a simple head movement but as a group of motions, linked to a specific behavior (behavioral bout) (Clark et al. 2016; Whalin, Weary, and von Keyserlingk 2021), then 28 head-bobbing bouts can be identified in the case period. Each bout (Mean duration ± SD = 2.34 ± 0.96/Mean VeDBA ± SD = 22.85 ± 9.54) consists of one to four head-bobbing events (Mean ± SD = 2.64 ± 0.78) and acquires a slightly higher activity level (10.23 VeDBA/s).

For the case of *D. jugularis*, we can observe that striking behavior presents a four-time higher activity level (VeDBA) per second than slithering (Table 2). A large portion of the hourly activity is spent with the animal remaining still in several interrupted events with a maximum duration of 1 min. Something interesting to note is that compared to *L. cypriaca* in which 90% of hourly activity is represented by the two studied behaviors above (i.e., running and head-bobbing), in the case of *D. jugularis*, the studied behaviors (i.e., attacking and slithering) could explain only 50% of its hourly activity. Analyzing VeDBA and digital camera records during the study period, we see that during the rest of the period (29 min; 48%), the species was moving on a very rough terrain. Those movements were constantly changing, not following a clear pattern, and difficult to be categorized under one of our identified movements.

4 | Discussion

Using tri-axial accelerometers and reference patenting, we have confirmed and archived 12 different movements and behaviors (33 variations) at a high rate (100 Hz) from two case study reptiles

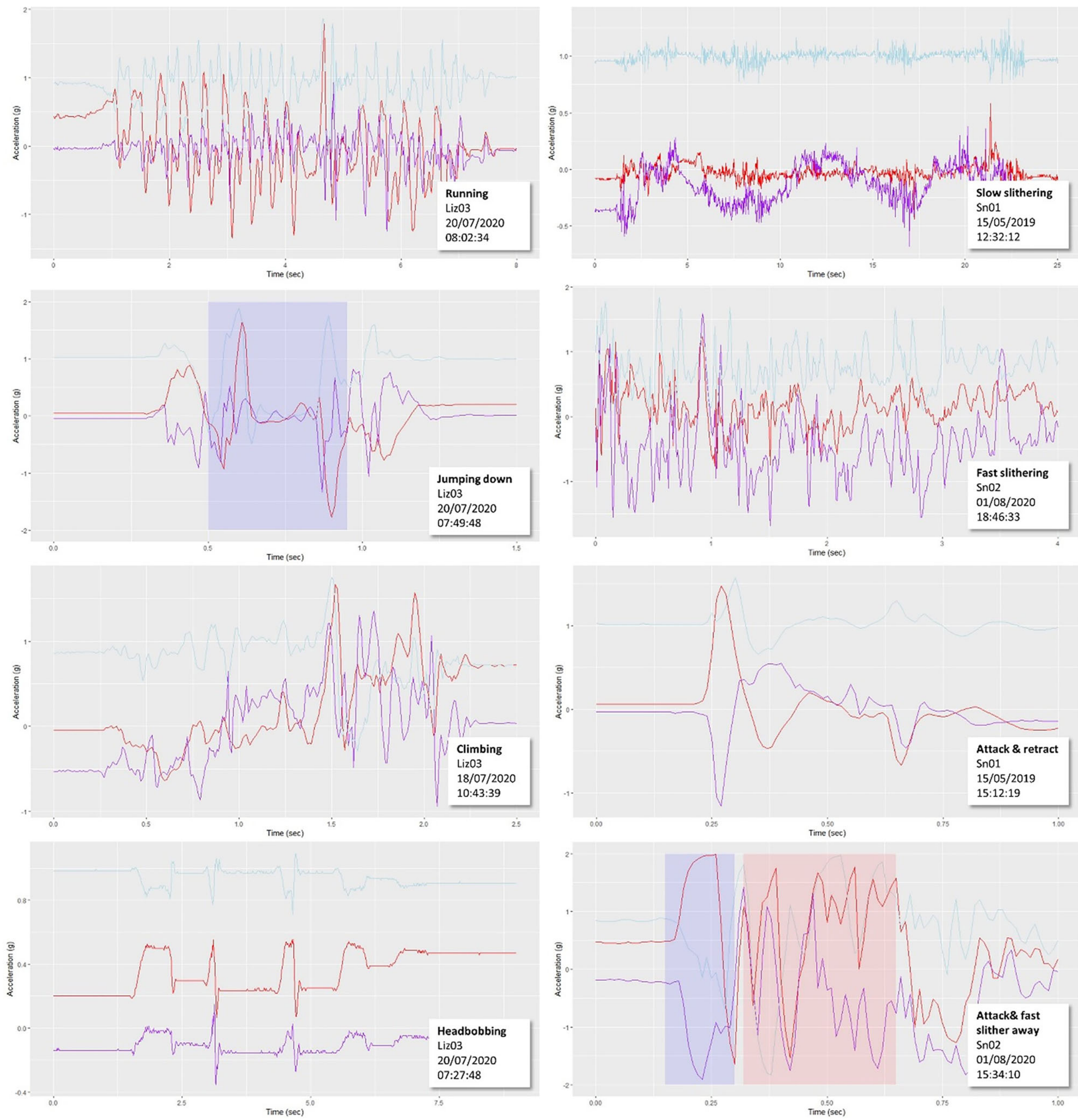

FIGURE 8 | Time series plots of 100 Hz tri-axial acceleration from indicative movements of the two case species (left: lizard *Laudakia cypriaca*; right: snake *Dolichophis jugularis*). Red line = surge (axis *X*); purple = sway (axis *Y*), and light blue line = heave (axis *Z*). Colored boxes indicate specific sub-second movements.

(lizard *L. cypriaca;* snake *D. jugularis*). The importance of our approach lies in its novelty offering for the first time the ability to extract behavior information from small lizards and snakes using accelerometers and motion capture (MoCap), despite the challenges posed by limited sample sizes. While our current results, derived from tests on only two individuals, may not fully represent the families of Agamidae and Colubridae, they highlight the potential of this technique. We acknowledge that additional challenges and constraints, not yet identified, may arise when applying this method across other taxa. Nevertheless, our approach demonstrates promising results and represents an important step toward understanding the behavior of not only these species but also other small terrestrial ectotherms with similar body shapes and locomotor patterns. Further testing and replication efforts will refine this technique, enhancing its applicability and utility across a broader range of species.

Thus far, behavioral analysis for related species for both the Agamidae (Ramos and Peters 2017; Strickland et al. 2021) and Colubridae families (Shine et al. 2000; Oda et al. 2022) have been conducted through traditional methods, such as direct behavioral observations, or technological approaches making use of cameras in natural or controlled environments (Wu et al. 2018; Rabosky et al. 2021). Through our approach, scientists could expand their

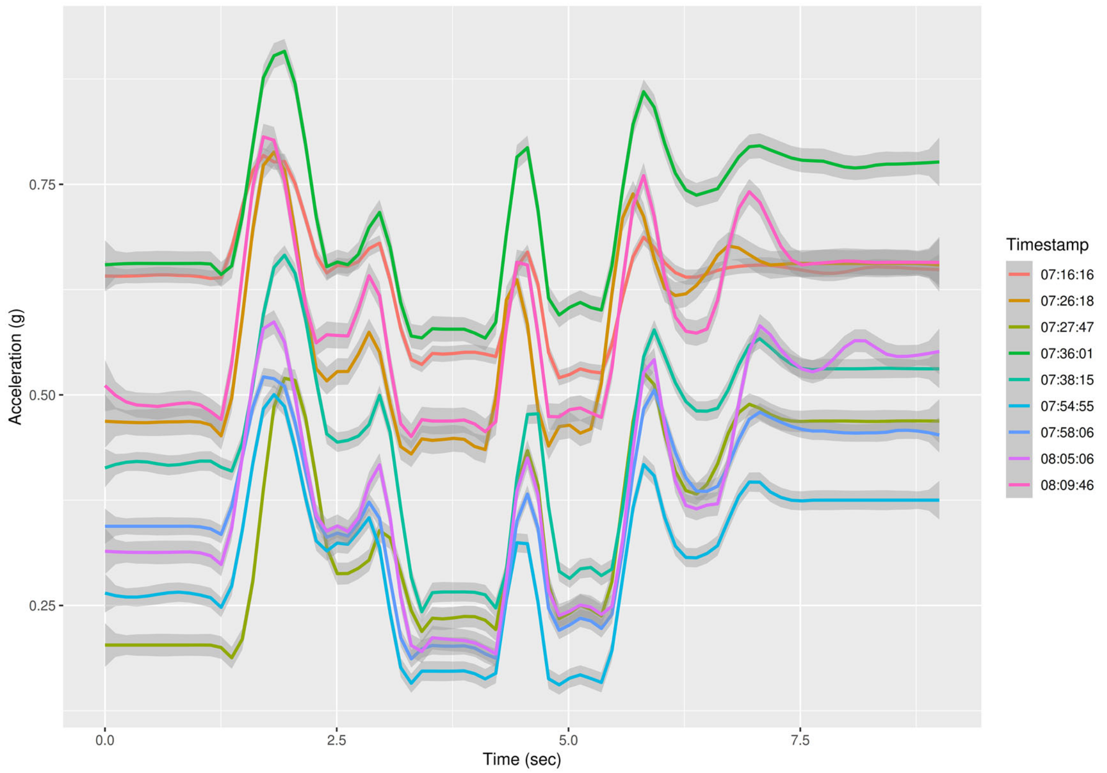

FIGURE 9 | Time series plots of 100 Hz surge acceleration from a unique behavior (headbobbing) conducted on 20/07/2020 by the same individual (Liz ID: Liz03D05), multiple times, a few minutes apart. The timestamp shows the initiation time of each headbobbing event. Despite the obvious difference in the acceleration, the movement's pattern remains the same.

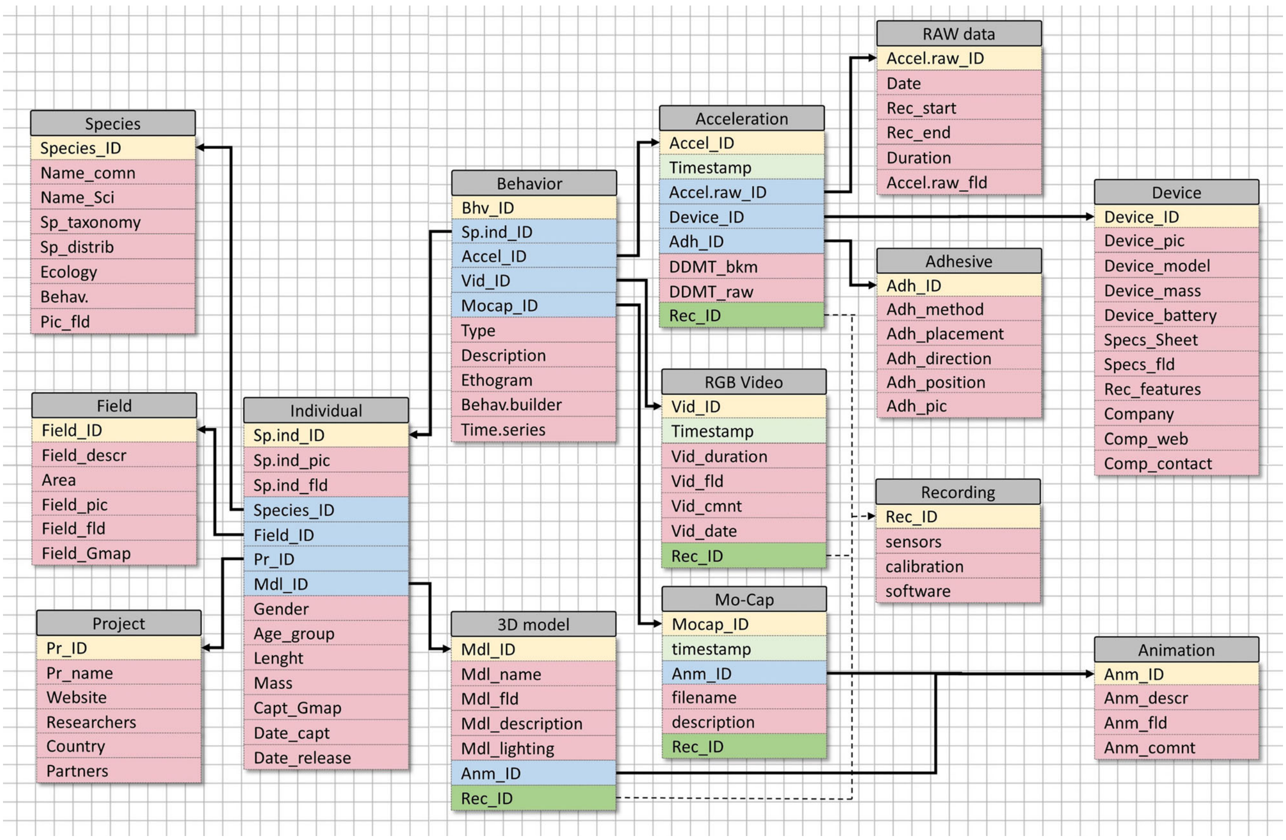

FIGURE 10 | Database diagram illustration, describing the structure and relation of the elements (data and metadata) included within the Behavioral Pattern Database.

TABLE 2 | Descriptive analysis of duration (s) and vector of dynamic body acceleration (VeDBA) as a summary of the amount of activity for the examined behaviors in the two case species.

	No. of behaviors identified	Duration (s)			VeDBA (g)			VeDBA per second
		Mean ± SD	Total	%	Mean ± SD	Total	%	
Lizard *L. cypriaca*								
Head-bobbing	60	0.81 ± 0.19	48.63	1.35	8.50 ± 2.92	509.83	3.90	9.54
Running	139	0.69 ± 0.59	96.90	2.69	46.35 ± 43.16	6489.60	49.62	66.97
Still/Resting†	146	21.42 ± 28.60	3127.20	86.87	13.31 ± 6.82	1943.62	14.86	0.62
Snake *D. jugularis*								
Striking	3	1.30 ± 0	3.90	0.11	106.68 ± 18.02	320.04	0.41	82.06
Slithering	76	6.56 ± 4.85	498.75	13.85	136.92 ± 107.25	10405.98	13.41	20.86
Still/Resting†	51	27.04 ± 35.63	1379.06	38.31	19.68 ± 20.07	1003.81	1.29	0.73

Abbreviation: SD: standard deviation. †Although practically still, as confirmed by visual observation, imperceptible acceleration values were recorded due to minor movements of the body. Those movements were not linked to any kind of behavior. After examination, a value of VeDBA < 0.015 was selected as a threshold for removing those values.

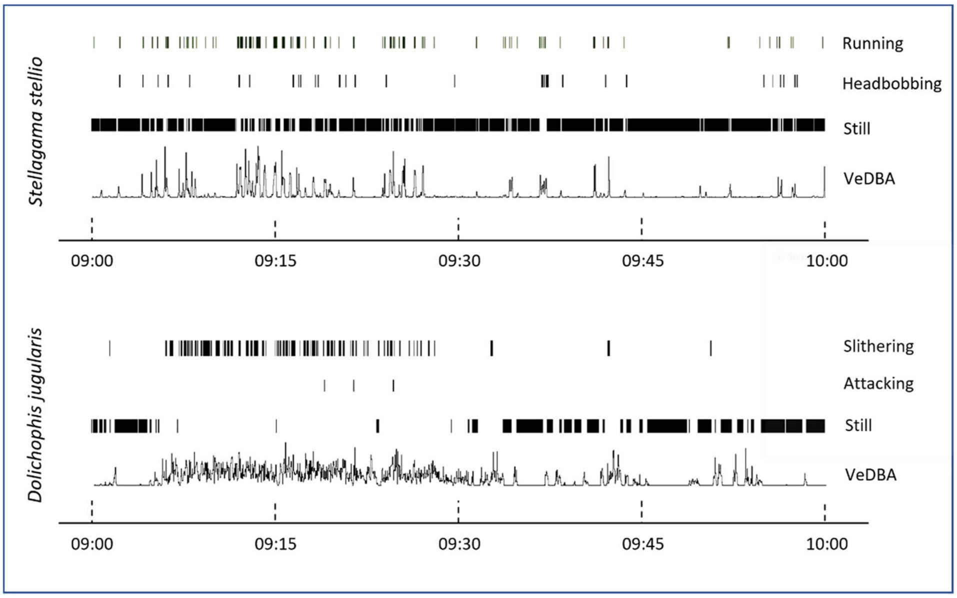

FIGURE 11 | Temporal imprint of two commonly identified movements (slithering for the snake and running for the lizard) and two distinct behaviors/signals (striking for the snake and head-bobbing for the lizard). Imprints are reported in the timeframe of an hour for the lizard species *Laudakia cypriaca* above (01/08/2019; 09:00 a.m. –10:00 a.m.) and the snake species *Dolichophis jugularis* below (30.07.2019; 09:00 a.m. –10:00 a.m.).

research to obtain, analyze, comprehend, and 3D archive high-rate behaviors and movements of small ectotherms. This novel dynamic can offer the scientific community the opportunity to analyze brand new datasets on ectotherms' movement that in turn could provide valuable information broadening behavioral (e.g., activity budgeting, predator–prey interactions), ecological (e.g., movement ecology, habitat use) and evolutionary studies (e.g., behavioral response to environmental change, parental investment), alike, in a similar way as it has already employed for other organisms (e.g., Wilson et al. 2006; Hammond, Palme, and Lacey 2018; Williams et al. 2018; Redcliffe 2021).

A critical asset for our approach was the recording at a high frame rate (100 Hz) and high sensitivity (±2 g). Given the fast movements of small lizards, a high sampling frequency is necessary to accurately characterize the pattern of acceleration (Shepard et al. 2009; Shiomi, Sato, and Ponganis 2012). In addition, slow walking movements (Barbuti et al. 2016) or sensitive movements of the head and jaws (Ydesen et al. 2014) might be lost when recording at low sensitivity. In our case study species, these two extremes are represented by the fast movements of lizard's running/snakes' striking (0.1–0.2 s) and the sensitive headbobbing signals of lizards (approx. 0.5 g). Most of the movements were adequately recorded and described. For the cases of extremely rapid movements, such as snake strikes, acceleration exits the borderline of 2 g. This extreme is recorded in the accelerometers as a rounding of signal at the max g, due to sensors averaging (see Figure 8). Future work on similar behaviors will need to consider carefully balancing the sensitivity threshold of their devices with the targeted behavior to be recorded and analyzed.

An important precondition for recording behavioral movements and signals in our case study species was the anatomical location of the attached accelerometer on the animals (glued in the dorsal area near the neck). The location of the accelerometer tag determines the type of behavior that can be recognized by the acceleration patterns (Brown et al. 2013). Our approach succeeded not only in identifying general movements (e.g., walking, running, climbing, and jumping) but also signal behaviors and detailed movements of the body that are extremely valuable in studying social interactions (Kaidanovich-Beilin et al. 2011; Doody et al. 2013). In the case of the lizard *L. cypriaca*, one of the main social displays of the species, that of head-bobbing, has been distinguished and separately analyzed from non-social behaviors. This, in combination with the extensive signal repertoires and territorial behavior of the Agamidae family (Fleishman 1992; Radder et al. 2006; Ramos and Peters 2016), shows that the use of accelerometers as described in our method can set a landmark for social behavior studies in small-size social ectotherms.

By taking a substantial leap beyond conventional techniques for assigning accelerometer waveforms to specific behavior categories (as outlined in Brown et al. 2013), our methodology advances through the utilization of high-rate (100 fps) recordings from optical MoCap systems to digitally reconstruct 3D motion. Beyond the evident applications in visualization (Tilmanne and d'Alessandro 2015; Zuffi et al. 2017), the heightened sensitivity of MoCap sensors in capturing motion information lends substantial support to the classification and analysis of animal behavior. This enhances the discernment of rapid signal behaviors, facilitating their more accurate recognition and description (Mathis et al. 2020; Labuguen et al. 2021). This capability gains even greater significance in the context of social interactions and signaling, where even the subtlest secondary motions (e.g., a slight turn of the head before fleeing away), often imperceptible to the human eye, hold immense import (Waters, Bowers, and Burghardt 2017).

A potential intrinsic advantage to our approach lies in its dual capacity: Both MoCap and acceleration data can serve as "labeled behavioral data" for training and evaluating classification models. Techniques like statistical learning classifiers (Tatler, Cassey, and Prowse 2018), decision tree analysis, and support vector machines (Glass et al. 2020) are potent tools for analyzing intricate and expansive datasets, but their application to animal movement remains infrequent (Grünewälder et al. 2012; Carroll et al. 2014). Currently, prevailing behavioral analysis and classification methods involve approaches like K-means (Chakravarty et al. 2019) or Boolean clustering (Wilson et al. 2018). Only recently have deep learning algorithms demonstrated their efficacy and significance in animal behavior through the analysis of acceleration data (Chambers et al. 2021; Arablouei et al. 2023). The combination of MoCap and accelerometer data leverages the power of supervised machine learning (ML) techniques, enabling machines to discern the behaviors of free-ranging animals. By doing so, it allows the construction of a comprehensive portrayal of reptile movement and behavior, even when direct observations or supplementary contextual data are unavailable (Kleanthous et al. 2022; Marcato et al. 2023). Unlike the customary practice in the literature, in which biologists assign specific discrete labels within predefined timeframes, ground-truthing acceleration data (Dentinger et al. 2022; Hoffman et al. 2024; Sur et al. 2023), the combination of MoCap and accelerometer operates within a continuous spectrum. As a result, this combination of techniques can depict movements not previously incorporated into the labeling schemes (Jiang et al. 2022; Yi et al. 2022; Ponton et al. 2023).

This capability opens avenues for documenting animals' movements and behavioral signals in their natural habitat, facilitated through a single accelerometer. This undertaking would involve mapping accelerometer readings to their corresponding MoCap equivalents and ultimately linking them to corresponding behaviors. Similar methodologies employed in domains like sports analysis and musculoskeletal rehabilitation researchers attest to the viability of this approach (Al Borno et al. 2022; Edwards et al. 2023). This procedure possesses the potential to unveil intricate social interactions, behavioral cues, and subtleties that frequently evade detection when relying solely on a solitary tri-axial accelerometer (Graf et al. 2015; Shuert, Pomeroy, and Twiss 2018).

As reported by Brown et al. (2013) if accelerometers are to achieve widespread use in studies of free-ranging wild species, there must be more complete reporting of methods, particularly for the classification phase of analysis, that are currently not adequately recorded. Already existing web-based platforms, with animal-borne telemeter data, such as MOVEBANK (https://www.movebank.org/) hosted by the Max Planck Institute of Animal Behavior and U.S. Animal Telemetry Network (https://oceanservice.noaa.gov/ocean/animal-telemetry.html), have been structured to support spatial data, mainly targeting movement ecology research and wildlife management. Although those databases are currently expanding their archiving processes, as well as adding accelerometer tools, there is still work to be done to fully incorporate and support behavioral research. In addition, existing databases focus on large charismatic animals (mainly marine and avian). Reptiles are mainly represented in those databases by marine turtles and large tortoises with only a few exceptions.

Taking these aspects into consideration, the developed BPD focuses on isolated behavior patterns and signals rather than collecting large amounts of movement information (GPS telemetry or large acceleration data set), which often produce extensive, confounded, and difficult-to-handle and comprehend datasets. Following an approach similar to spectral signature databases (Hueni et al. 2009; Plamondon et al. 2014), which highly altered and revolutionized remote sensing (Angelopoulou et al. 2019; Sun et al. 2020), we aim to develop a database consisting of behavior signatures, which can be used to improve and advance behavioral recognition and analysis, eventually assisting replicability of behavioral research among researchers.

An essential aspect of our methodology involves the integration of animals and their recorded behaviors into immersive and high-fidelity animated 3D models. This builds on and enhances existing works such as the ones of Irschick et al. (2020, 2022) where, although accurate 3D models of living animals have been developed, movement data have not yet been integrated. Beyond its utility in scientific research, the visualization of animal movement and behavior extends its impact to the realm of innovative environmental education. This fact is underscored by the establishment of the Cyprus 3D Reptiles Museum (https://3dreptiles.cs.ucy.ac.cy), a platform that showcases reptilian visualizations in striking clarity and realism within a three-dimensional environment (Zotos et al. 2022). Our approach, by combining cutting-edge technologies with the intricacies of animals' movements and behaviors, coupled with synergistic endeavors such as Digital Life (http://digitallife3d.org), holds promise to strengthen and enhance efforts aimed at documenting and preserving the intangible heritage of life on Earth.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data used in the paper as well as data archived on the Behavior Pattern Database are available upon request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.