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Fly with the flock: immersive solutions for animal movement visualization and analytics

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Understanding the movement of animals is important for a wide range of scientific interests including migration, disease spread, collective movement behaviour and analysing motion in relation to dynamic changes of the environment such as wind and thermal lifts. Particularly, the three-dimensional (3D) spatial–temporal nature of bird movement data, which is widely available with high temporal and spatial resolution at large volumes, presents a natural option to explore the potential of immersive analytics (IA). We investigate the requirements and benefits of a wide range of immersive environments for explorative visualization and analytics of 3D movement data, in particular regarding design considerations for such 3D immersive environments, and present prototypes for IA solutions. Tailored to biologists studying bird movement data, the immersive solutions enable geo-locational time-series data to be investigated interactively, thus enabling experts to visually explore interesting angles of a flock and its behaviour in the context of the environment. The 3D virtual world presents the audience with engaging and interactive content, allowing users to 'fly with the flock', with the potential to ascertain an intuitive overview of often complex datasets, and to provide the opportunity thereby to formulate and at least qualitatively assess hypotheses. This work also contributes to ongoing research efforts to promote better understanding of bird migration and the associated environmental factors at the global scale, thereby providing a visual vehicle for driving public awareness of environmental issues and bird migration patterns.

Keywords:
animal movement analysis, immersive analytics, collective behaviour, virtual reality, augmented reality

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1. Introduction

Movement is considered a fundamental biological property of all living beings and biological processes. From molecules within cells to whole populations across continents, biology is defined by movement. At the organismal level, movement allows, in particular, animals to cope with the fluctuations in their environment and to seek suitable environmental conditions. Studying animal movement is consequently at the centre of understanding how animals interact with their environment and how changes in conditions affect individuals. Movement is also the underlying process in colonization, juvenile dispersal, gene exchange and ultimately speciation [1,2]. Some other consequences of movement are disease dynamics where pathogens are moving by exploiting the movement capacities of their hosts with sometimes great economic and human health impact [3–5]. Hence, there has been an increasing need to document and understand the causes and consequences of animal movement.

With technological innovations in miniaturization and dropping costs of tracking units, ecologists are now increasingly in the position to equip a larger number of animals with tracking devices, particularly in the wild [6]. These new devices are continuously becoming smaller, lighter, and often not only report position but also carry additional sensors (measuring accelerations, temperature, magnetic field, etc.). They can be equipped with solar panels and stream data live through mobile phone networks [7]. With tracking devices transmitting ever more dense data from more individuals moving across greater ranges remotely, the discipline of (movement) ecology is on the verge to transition from a data scarce to a big data discipline. The increased ease with which ecologists can track animals and collect additional data through sensors not only deepens their understanding of movement and behaviour in the field, it predominantly challenges the classical analytical approaches. A particular challenge in movement ecology is the analysis of movement data of animals using the vertical dimension when flying or diving (swimming). Even simple tasks of data visualization, exploration and manipulation prior to statistical analysis can become challenging due to the four-dimensional characteristics of movement (three spatial dimensions through time) heightened by the increasing volume of data [8].

Advances in display technologies and visualization platforms provide several options for interactive and immersive visual representations particularly suited for movement analysis. The young field of immersive analytics (IA) aims to develop methodologies for collaboration, interaction, visualization and analytics to support reasoning and decision-making in immersive environments [9,10]. Classical automated analyses, e.g. statistics and clustering, are integrated into these environments to allow the analysts to interactively explore the data and to create and falsify hypotheses. However, the requirements for presentation and IA on the recent large display walls and virtual reality (VR) and augmented reality (AR) platforms, have not yet been thoroughly investigated, thus creating a gap for visualization designers and researchers alike. Here, we present a practical overview and comparison of potential platforms of different three-dimensional (3D) immersive environments for explorative visualization and analytics of bird movement data. We investigate the requirements and challenges of visualizing movement data of large migratory bird species for presentation and analysis, and discuss the characteristics, benefits and shortcomings of the available technologies in the context of the implemented prototypes. While we focused on bird data, the findings and also the solutions obtained in our projects can be transferred to the analysis of other taxa with only small adjustments.

Display technologies such as CAVEs [11] (immersive hybrid reality environments that allow physical collocation of multiple users), large-scale tiled 3D display walls [12], PowerWalls [13] (large high-resolution devices) and head-mounted displays (HMDs, devices worn on the head with a small display in front of the eyes, such as HTC Vive and Google Cardboard) [14] have shown significant improvements in the last decade, e.g. regarding resolution and tracking capabilities. They have advantages (screen area, resolution) over traditional single panel displays especially when viewing dense information such as GPS trajectory data. Immersive 3D technologies, being increasingly affordable, are appealing platforms for both visualization applications and public outreach. These technologies have had some success in promoting public awareness in other fields, such as biomedicine [15,16] and ecology [17], and were applied in prototype implementations, e.g. in biochemistry [18] and biomedicine [19].

Applications like the 3D molecular framework UnityMol [20] showcase how the potential of new technologies can be exploited by turning the traditional role of the computer from an aide to compute and list abstract data into a virtual laboratory provider. Users can directly interact with their data in a variety of representations, and explore it in the context of additional information that is required for a deepened understanding. Such approaches begin to change the way data are represented and analysed, and have the potential to greatly improve the efficiency with which new insights can be derived. In addition, these new approaches do not require the analysts to also possess expert skills in the design and development of interactive graphical representations. However, applications in biology are still sparse, and IA research is focused on fundamental questions using abstract tasks [21].

There are already solid foundations for visual analytics of movement data [22], and visualizing animal movements is a cross-disciplinary research opportunity for biologists and computer scientists that holds much promise for both parties [6,23]. However, visual and immersive analysis of animal behaviour is a relatively under-explored area, even though tracking, for example birds, by satellite positioning started as early as the 1980s [24]. These tracking studies have deepened understanding of migration [25], navigation [26,27], flight patterns [28,29] and foraging strategies of birds [30]. High-resolution sensor data can also be used to derive further information on the environmental conditions, e.g. meteorological conditions [31]. The interactions between moving individuals have been recently begun to be studied in free-living animals [32–34]. Visualization of 3D movement data can help scientists to work towards making significant advances in animal movement research [35]. Cheap, light-weight, high-resolution tracking technology now provides the data, analytic challenges and questions to be handled and approached using immersive 3D visualization technologies.

Immersive data visualization presents a number of potential benefits for animal movement analysis:

- Movement happens in a specific environmental and behavioural context, experiencing this context and seeing the synchrony between *actio* and *reactio* can help to develop and sharpen a working hypothesis. The volume of data is, however, sometimes so overpowering that finding the special ‘moments’ and linking them efficiently to other candidate sources of data, a necessary precursory requirement for analysis, becomes tedious.
- The representation of the context in which the movement happened additionally helps the analyst to more intuitively assess basics such as consistency and potential data quality problems, allowing data to be interactively validated and results in the reference frame of the environmental context. Challenges like the uncertainty that is introduced by the quality and coarseness of the sensor data can thus be recognized and tackled more efficiently.
- Immersion in movement data can also provide access to the sensory capacities of the study system. Thus, it allows better integration between the physiological and neurological

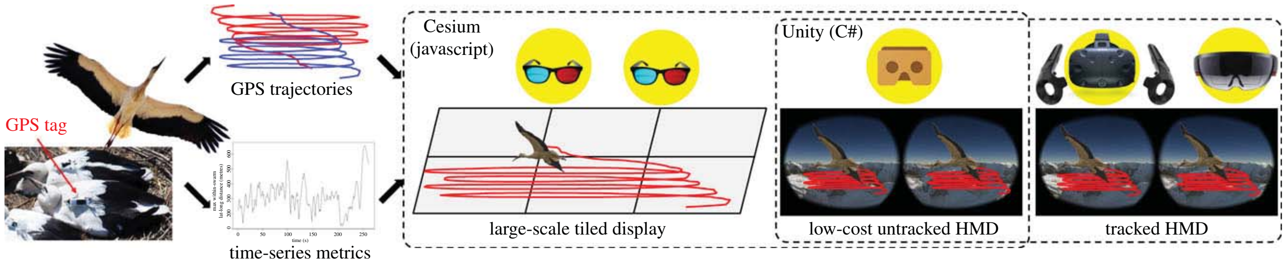


Figure 1. One dataset, multiple immersive environments. A typical set-up of a sensor for movement and other (e.g. temperature) data acquisition attached to a bird. The data are transferred via the GSM (mobile phone) network, and then visualized in different immersive environments for comparison. These environments are realized by making use of different underlying software, e.g. the geographical visualization library Cesium and the 3D development platform Unity, and also different hardware devices, e.g. tiled display wall or head-mounted displays (HMDs). The hardware platforms supported by Cesium and Unity overlap, as both allow creation of mobile VR solutions, e.g. based on Oculus Go or Google Cardboard.

aspects under which movement was completed, giving access to more hitherto inaccessible dimensions of the data in an intuitive and reproducible way, enabling relevant questions to be asked.

— Immersive environments can support natural and more intuitive interaction with the data, compared to a classical set-up with a desktop display, keyboard and mouse.

At this new research frontier, we perform a benchmark study by employing a real-world dataset in multiple immersive environments (figure 1), with two main goals: (i) create prototype visualization tools for biologists, forming the basis for further IA applications and (ii) inform the 3D visualization community on design considerations. Making use of a unique tracking dataset of a group of flying white storks, we provide the opportunity to explore different tools that allow the investigator—to various degrees—to ‘fly with’ and learn from their animals. After an initial short report of first findings during the development phase [36], we present here the results from the first major step of our ongoing research project.

In §2, we describe use cases and user requirements for avian movement analysis, the data used in the study as well as the immersive environments under comparison. Section 3 presents the results of our comparison and an expert study, §4 a short discussion of the results.

2. Material and methods

We developed prototypes of IA environments for exemplary classes of environments to cover the range of potential hardware to be used in future analytics workspaces, including tiled 2D/3D display wall, mobile VR, tracked VR, and AR. For these environments, state-of-the-art hardware devices were used in combination with software for representation, analysis and interaction which we developed using suitable software frameworks and platforms.

2.1. Visual encoding, user requirements and use cases

In 3D immersive environments, we can present the four dimensions of space and time via 3D visualization and dynamic animation, and encode additional dimensions by integrating data visualization techniques [37,38], e.g. by mapping data on visual cues such as colour. Interactivity, key for analytics in visual as well as immersive environments [39], allows expert users to show or hide visual elements to produce a custom data view. A major challenge in IA research is the combination of interactive visualizations of abstract and spatial data in an intuitive user interface.

Within this project, we collaborate with researchers from biology in order to understand their requirements for analyses and use-cases. In an informal expert review, we collected information on their research questions, data availability, current analytical tools and work-flows. We identified three main use cases: (i) exploratory analysis, (ii) hypothesis testing and (iii) outreach for presenting the collected data to decision-makers and the lay public. For the first two use-cases, sub-cases for single-user and collaborative analysis need to be distinguished, as specific requirements have to be considered when more than one user is involved, e.g. regarding tracking, view perspective, collocation and avatar representation in virtual environments. In addition, the research questions under investigation might differ quite significantly with respect to the details that need to be shown for different aspects of the bird behaviour, and regarding the level of analytics involved. As an example, the detailed analysis of collective behaviour might focus on long-range movement and recurring behavioural patterns when studying seasonal bird migration, whereas a local thermal exploration analysis might include a leader–follower analysis parameterized to fit the specific local environmental and bird information.

Biologists collect bird behaviour data together with influence factors that might be important, for example, for bird decision-making and collective behaviour, to infer the mechanisms behind this decision-making and communication in groups. For our expert groups, the data under investigation are usually a combination of sensor data from tagged birds and environmental data, mainly on weather and geographical information. In the specific example of the white stork tracking study, the data are a combination of movement GPS and environmental data (e.g. wind) [40]. GPS data are often only available for short time bursts. Influence factors include terrain, vegetation, weather, distance travelled, individual physiological properties and health. Some of this information is known, e.g. high-resolution terrain information is available for many regions, most of it, however, has to be estimated or derived from the sensor data. While wind, and in particular, thermals are important influence factors for analyses, there is usually no directly measured data available—especially not for different atmospheric layers—and it has to be derived, e.g. by dead reckoning from the bird movement. Although atmospheric conditions are a crucial factor influencing bird movements, these data are sparse and hard to measure. Thus, deriving wind conditions from the birds’ movements is important, and good visualization techniques can assist on that. As an example, see figure 2, where the drifting of the thermal column at different altitudes is shown by the corresponding behaviour of the different flock members.

Allowing researchers to put themselves in the position of a bird provides opportunities to understand the decision-making process of the flock, or the intricate differences between individual flock members while moving at small and large spatial scales.

A central class of research questions is concerned with the collective behaviour of birds in a flock—how does the behaviour of other birds influence the behaviour of an individual? Birds

Figure 2. Different perspectives on the same dataset using the synchronized visualization in multiple browser windows (*a*, top view, *b*, side view). The side view shows the marking of the currently fastest climbing bird by a sphere and the climbing profile of the selected bird.

Table 1. Bird trajectory data used in this study. Primary (measured) data are indicated with the green block, secondary (derived) with red, additional influence factors used in the analysis with blue.

	variable	description
🟩	time	time stamp of sensor measurements
🟩	bird ID	ID of the tracked bird/sensor
🟩	lat	measured latitude
🟩	long	measured longitude
🟩	alt	measured altitude
🟩	ground speed and heading	GPS velocity
🟥	direction	movement direction from track points
🟥	wind	wind velocity estimates [41]
🟥	distances	distances between birds
🟦	terrain	
🟦	vegetation	
🟦	visual field	

seem to perform tasks differently in roles that they take on for a certain period of time, e.g. as a leader that explores a thermal for the flock. One question then is how such an exploration is performed, while the question related to the collective behaviour would be how other birds can profit from this exploration, and what their decisions are based on. Another question relates to the visibility network—which birds see others and can use this for faster reaction, for example, when the swarm gets attacked by a predator.

2.2. Data used in this study

The data used in this study were collected using miniaturized GPS sensors (figure 1) as described in [7,41]. The GPS data consist of geographical position and elevation in World Geodetic System (WGS84) coordinates speed and heading (table 1). Raw data were obtained in Keyhole Markup Language (KML), an international standard of the Open Geospatial Consortium, compatible to multiple geographical visualization platforms. The data used are now partly freely available from Movebank [42].

2.3. Visualisation on a tiled two- and three-dimensional display wall

To visualize geographical data in large-scale tiled displays without sacrificing resolution, we first used the Google Earth platform. Google Earth fully supports large-scale high-resolution displays such as the CAVE2 environments [43]. However, this proprietary platform limits the capabilities to manipulate visualization features, and neither Google Maps nor Google Earth can visualize KML data in combination with stereoscopic 3D (S3D) rendering, an important requirement for immersive analysis [44,45]. Therefore, they are excluded from the following analyses.

In order to have a flexible and open framework that also supports S3D rendering, our display wall visualization approach is based on the open source cross-platform Cesium, a geographical visualization library [46]. It supports tiled displays, the KML format, the HTML5 standard and stereoscopic rendering (figure 3). In addition, the visualization can be distributed over different browser windows, enabling the visualization of individual bird behaviour side-by-side (figure 2). The multi-view set-up was tested in our laboratory on a display wall that consists of six 55 inch monitors supporting passive stereoscopic visualization (figure 3). Different monitors could show different perspectives of one or many birds, or first-person perspectives of six different birds. While the software implementation is flexible to suit different hardware set-ups, our set-up is a good compromise between screen space and the viewing distance required, visualizing both details in high resolution and the full picture on all displays without much body movement.

The viewing parameters like time and clock speed are synchronized across the different windows. This synchronized visualization was achieved by adapting the Liquid Galaxy support for Cesium to our needs [47]. In a preprocessing step, the bird data are automatically analysed to allow a mapping of information that might be of interest for investigation to visual cues, e.g. by marking the bird with the highest climbing speed at a time point, or by giving an indication of distances in the flock, the estimated ground wind speed [41], the flight speed or track length by using colour coding. Additional data like altitude profiles can be shown using diagrams, which are implemented using the D3 library.

2.4. Low-cost untracked mobile virtual reality visualization

The Cesium-based semi-immersive visualization of bird trajectories on the tiled 3D display wall presents a community-viewing environment. With the maturity of VR headsets (HTC Vive, Google Cardboard), it is a natural development to extend this semi-immersive to a fully immersive environment, allowing users a 360° experience. A major design decision then is to implement either a solution for a tethered and tracked VR headset, which also requires a dedicated computer to drive it, or a solution for untracked, but lightweight and portable devices like Google Cardboard or Oculus Go. Google Cardboard-based solutions allow mobile VR visualization that only require a mobile phone, and

Figure 3. Stereoscopic visualization of the bird trajectories using Cesium VR as a server and a tiled 3D display wall with polarized glasses as a display client. Tiled displays can be used for one large view or for comparisons of different views as shown here.

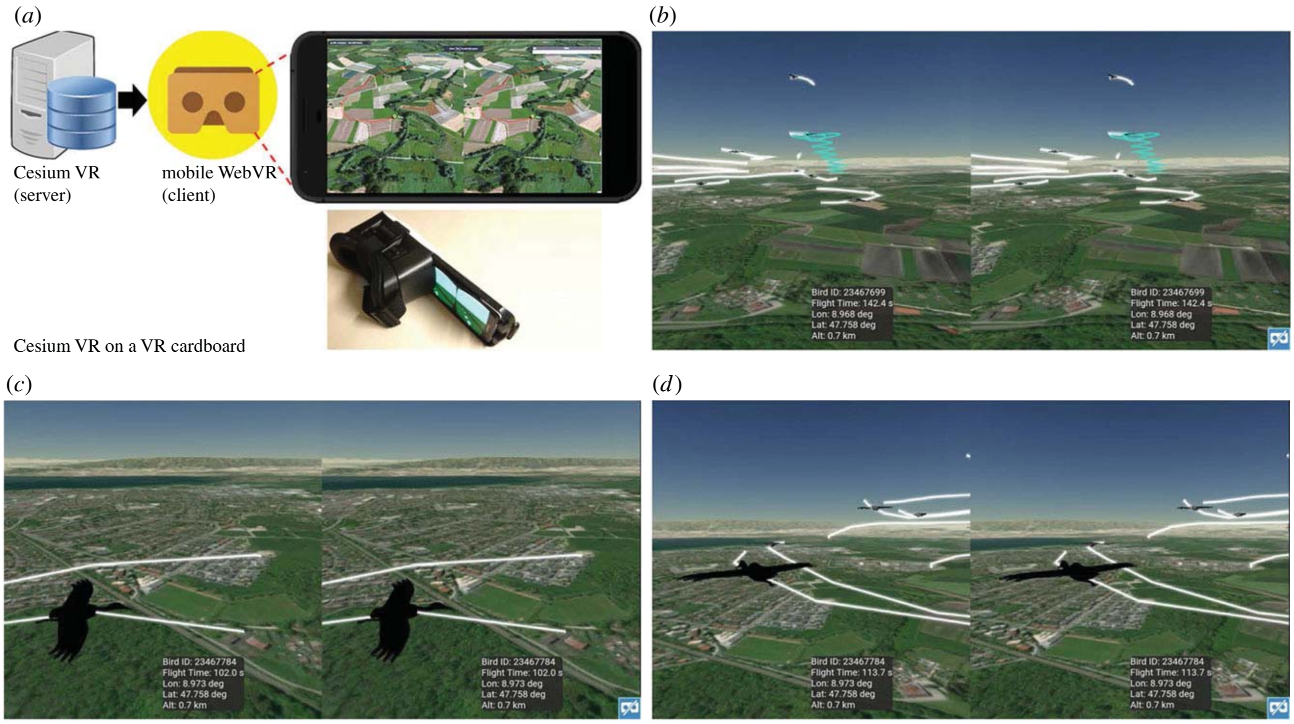


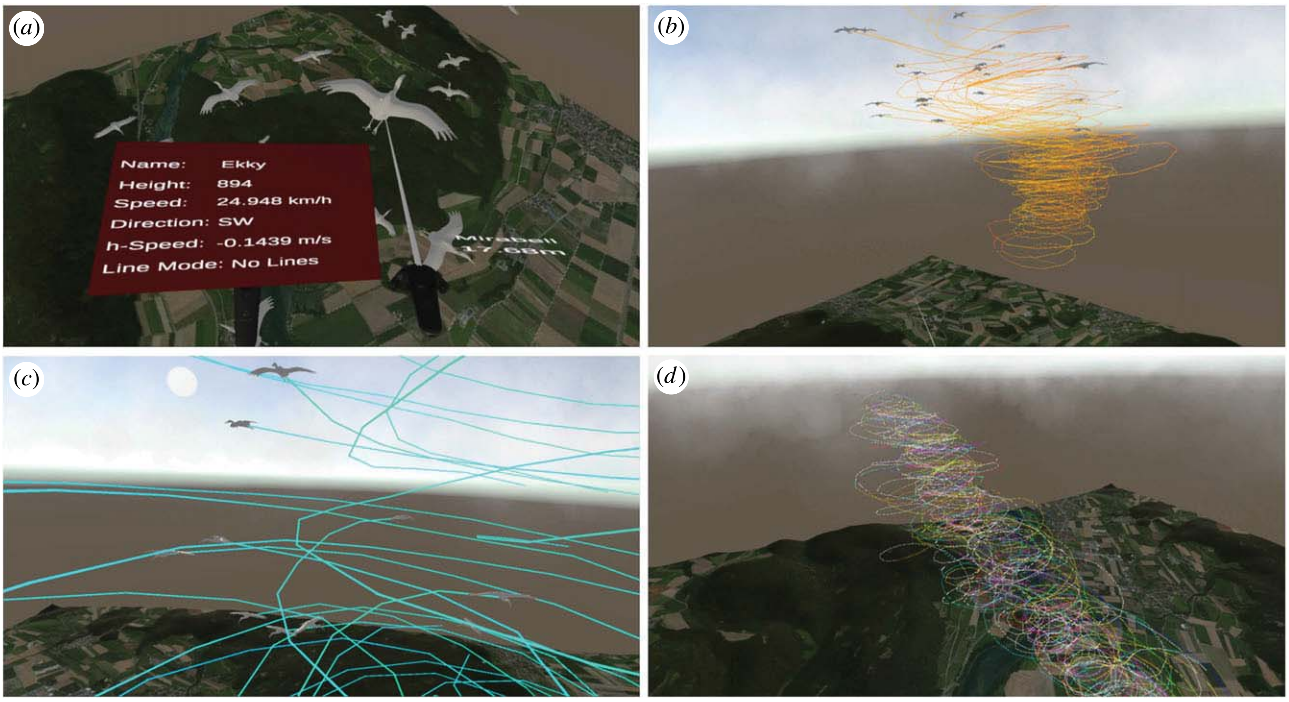
Figure 4. Fly with the flock: visualization of a flock of storks with Cesium on the web. The side-by-side images illustrate the stereo view using a Google Cardboard as shown in (*a*). (*b*) An overview of trajectories visualized using Cesium, including climbing a thermal. (*c*,*d*) Close-ups of a single stork flying along the track (*c*) after 102.0 s, (*d*) after 113.7 s flight time). The info panels show the ID of the selected bird derived from Movebank, the actual flight time, the longitude, latitude and altitude.

thus can also be used in the field. While not providing tracking of the analysts motion, they still support head-tracking, i.e. the analysts can move and turn their heads to explore different viewing directions in the 3D environment.

Cesium was also chosen for our untracked mobile VR headset-based approach, as it is optimized for the use with current mobile phones. However, as of Cesium v. 1.42, there was no fully functional VR implementation available. Therefore, we combined unreleased bug fixes with our new implementation to be able to provide a fully functional head-tracked version. Potential rendering clients for Cesium on the mobile phone are a number of current Android-compatible web browsers, such as Google Chrome$^{\mathrm{TM}}$ or Firefox. Since importing and displaying geographical data in Cesium is a rather simple task, changes to the presented data can be quickly implemented.

Using an Android device with a VR headset like Google Cardboard only allows viewing of simple 3D objects due to its relatively slow processors (figure 4*a* for the set-up). There are two options to run the application: it can connect to a server via IP address (figure 4*a*) or to a server installed locally on the smartphone. Using an external back-end server, the frame rate of the imaging content can be maximized to improve the mobile visualization experience.

Without additional technologies, position tracking is not possible in this environment. Therefore, only the smartphone's movement can be directly translated to perspectival changes. For navigational purposes, external input devices are required. In our set-up, a Sony PlayStation 4$^{\mathrm{TM}}$ controller was connected via Bluetooth to the smartphone. Navigation is done by moving the camera forward into the direction of the user's viewing direction. In addition, the controller is used to map different functionalities to the buttons, such as switching between individual birds, locking or unlocking the view to a single bird. To show relevant information a heads-up display is used with some important values to give the user information about the current bird, its actual flight time, the location, etc.



Name: Ekky
Height: 894
Speed: 24.948 km/h
Direction: SW
h-Speed: -0.1439 m/s
Line Mode: No Lines

Figure 5. Fly with the flock: visualization of a flock of storks in VR. (*a*) Perspective of the bird called 'Ekky'. Information about the current bird is shown on a panel on the left-hand controller. The right-hand controller shows the distance to bird 'Mirabell'. (*b*) Perspective of the external observer, line colour maps to ground speed. (*c*) Perspective of a bird, trajectory colour maps to height speed. (*d*) Perspective of the external observer, trajectory colour maps to one colour per bird.

Figure 4 shows different perspectives of a bird flock: figure 4*a* shows the architecture of our solution, figure 4*b* an overview of trajectories of the complete flock, figure 4*c*,*d* shows close-up perspectives of a single selected bird. The shown data were downloaded from the Movebank repository. The information frame is showing the bird's Movebank ID, as well as the actual position and flight time.

The major advantages here are the widespread availability to many users as well as low costs; while the disadvantages are low visual quality, low immersion and restricted interaction.

2.5. Tracked virtual reality visualization

The tracked VR implementation lets the analyst step into the world of a flock in a fully immersive environment. By taking over the view of one of the birds (figure 5*a*,*c*) or flying around the flock as an external observer (figure 5*b*,*d*), the analyst can examine the flock from an internal or an external view. Besides the representation of the landscape, based on satellite imagery and terrain information, the implementation provides various tools to derive information from the simulation. We used the HTC Vive VR headset for our realization which provides a high degree of immersion with room-scale tracking using two mounted base stations, and two hand-held controllers. The interactive visualization of the movement data was implemented using the Unity development platform. On start-up, the movement data are loaded and the mean coordinates are calculated. A request to *MapBox*[1] with these coordinates results in the display of the original topography where the data were recorded. The map dynamically extends as the flock moves on. For each bird in the data file, an appropriate bird model is loaded (figure 5). According to the recorded data, these models show realistic moving behaviour. The Vive hand-held controllers are used for interaction with and navigation in the virtual environment, allowing the analyst to obtain information about the birds and to move in the virtual world. One of the controllers is a distance metre, showing the distance to the object that is hit by a 'laser pointer' (figure 5*a*). The other controller shows information for the current bird that the analyst flies with, including name, current altitude, ground speed, heading and climbing speed. For interaction, the analyst can stop the simulation. This allows an in detail investigation of the current constellation. A teleport function allows the user to take over and change the perspective of any bird. The simulation starts always without trajectory lines to avoid a crowded visualization on start-up but visualization of the tracks and additional data can be triggered on demand. In order to show the flock movement over time, we introduce three *line modes*. In line mode *per bird* every bird has its own colour for an easy distinction (figure 5*d*). The line mode *ground speed* maps the current speed of a bird over ground (figure 5*b*). *Height speed* maps how fast the birds gaining height (figure 5*c*). The colours are normalized per bird and then interpolated between the extremes. To examine the flock from an external view, the analyst can jump to the so-called *observer mode* to move freely. Thus, the flock movement over time with the trajectories drawn for the whole flock can be clearly seen (figure 5*b*,*d*).

A video of the VR-based interactive visualization is available at [48].

2.6. Tracked augmented reality visualization

To tackle the spatial tethering constraint of the HTC Vive headset, we implemented bird trajectories visualization on the Microsoft Hololens mixed reality platform. By using a transparent display, the Hololens enables viewers to see a complex scene combining both virtual object and the real-world environment, while allowing the users to similarly walk between the bird trajectories to investigate the data using hand gestures. The implemented software environment is based on the previously mentioned tracked VR visualization. The emerging class of untethered tracked AR headset such as the Hololens presents a promising step towards making fieldwork AR/VR feasible, but is still hampered by several shortcomings. First, current devices have a very narrow field of view, which make the immersion inferior to the VR solutions. Secondly, existing AR goggles have only low outdoor contrast, which restrict their use in fieldwork considerably. Moreover, due to the lack of powerful input and feedback devices, like the Oculus' or HTC Vive's controllers, they only allow for very

Table 2. Hardware design consideration, developer's perspective (top) and expert user's perspective (bottom). Five expert users were asked to rate different aspects of the environments on a five-level scale from excellent quality (++), good (+), acceptable (o) to poor (−) or inappropriate/not available (− −).

	S3D tiled display	mobile VR	tracked VR	tracked AR
example device	S3DWall	Google Cardboard	Vive	Hololens
developer's perspective				
ease of set-up	−	++	+	+
haptic feedback	− −	+	++	− −
field of view	+	+	++	−
S3D quality	+	o	++	+
expert user's perspective				
visual quality	++	+	++	o
ease of interaction	++	++	++	o
immersion quality	+	+	++	+
cost effective	−	++	++	o
regular use	++	++	+	o
short term (<1 h)	++	++	++	++
long term (≥1 h)	++	o	−	
collaboration potential	++	o	+	o

restricted interaction, which can lead to a slow and tedious analysis process. Finally, they require a stable internet connection, which is still not feasible in many working environments for animal movement analysis. On the positive side, models of data representation in 3D software like Unity for use with a VR HMD can be relatively easily transferred to current AR devices like the Hololens. However, how the visual representations should differ has to be more thoroughly explored to fully exploit the potential of the devices.

3. Results

3.1. Comparison and design considerations

From the 3D visualization developer's perspective, we summarized the experience of constructing bird movement visualization, which can also be informative for visualizing other types of 3D data. Design considerations for 3D immersive visualization hardware are shown in table 2, where the different hardware is broadly categorized as S3D tiled display (tiled 3D display wall), mobile/untracked VR (Google Cardboard), tracked VR (Vive) and tracked AR (Hololens). In addition, design considerations for software development platforms are summarized in table 3, where three main platforms (Google Earth, Cesium/WebVR, Unity) employed in this work are compared and contrasted. While all three software platforms are VR ready, Google Earth VR is currently not IA ready, as it does not support the inclusion of further external data.

3.2. Expert evaluation

The realization of the immersive environments was achieved in close collaboration with our biologist collaborators, who gave input for all major design decisions and also feedback for our corresponding implementations. In order to evaluate the potential of the different environments at the prototype stage and to put them in context, an expert study with five subjects was conducted, using each of the previously discussed technologies. The guided discussion was accompanied by a questionnaire, evaluating the properties shown in table 2 bottom. The corresponding table section summarizes the feedback of the expert users, estimating their expectations towards the different hardware set-ups. Each of them was shown the four technologies: (i) tiled 3D display wall, (ii) the untracked mobile VR, (iii) the tracked VR and (iv) the tracked AR. The environments then had to be judged based on a number of criteria: (i) visual quality, (ii) ease of interaction, (iii) immersion, (iv) cost-effectiveness, (v) regular use, (vi and vii) suitability for short-term (less than 1 h) and long-term (greater than or equal to 1 h) use and (viii) potential for collaborative analysis.

Table 3. Software design consideration, from the developer's perspective, rated on a five-level scale from excellent quality (++), good (+), acceptable (o) to poor (−) or inappropriate/not available (− −). (D)esktop, (V)R release, (W)eb. The ✗ and ✓ symbols indicate if a feature is missing or available, respectively.

	Google Earth	Cesium	Unity
visual quality	D+/V++	o	+
ease of expansion	− −	o	++
platform maturity	+	−	++
custom data?	D✓, V✗	✓	✓
installation?	D, V✗, W✓	✗	D✓, W✗
open source?	✗	✓	✗/✓

In addition to the expert study, we also collected informal feedback from a larger number of biologists visiting our lab. The expert feedback provided valuable comments and assessment supporting the future development of new VR/IA platforms for 3D bird movement. The fully immersive HMDs were considered the best technology in terms of immersion and visual quality. But all HMDs, as well as the Hololens and Google Cardboard, are problematic in that the subjects did not expect to use them for longer periods (greater than 1 h) as required for specific tasks. In addition, Vive and Hololens are spatially tethered and in case of Vive confined to a room-based indoor environment with mounted tracking sensors. Regarding motion sickness, a typical problem of VR environments such as that of Vive, by showing the real world in the background, Hololens had the biggest advantage. In terms of visual quality, HTC Vive was found to be superior to Google Cardboard, which was considered superior to Hololens. Regarding viewer comfort (regular use), HTC Vive was found to be superior to Hololens, but can be inferior to Google Cardboard. The tiled 3D display wall cannot provide full immersion, but the visual quality is among the best, allowing long-term use. However, the downside is its substantial cost.

Also, the expected visual quality of bird visualization strongly depends on the application case: an icon-based visualization as known from Google Earth (and also possible in Cesium) is sufficient for a global flock analysis. An abstract box-like visualization is appropriate in case the bird's orientation is irrelevant or uncertain. More complex and animated visualizations like the ones used in tracked VR and the tiled display environment are only relevant in cases where the required data are available or predictable with high certainty (figure 5). A fully textured photo-realistic bird model is usually not required unless for outreach. However, animation including wing flapping can be helpful to domain experts to study particular aspects of bird motions and flock behaviours and could in the future be empirically derived and included in the visualization using existing onboard sensors such as accelerometers and gyroscopes.

In terms of collaborative work, the participants concluded that the tiled 3D display wall was very promising. Their opinion was more diverse regarding the other technologies, as for VR the real world as well as the collaborators were not (fully) visible and for the recent AR technologies, the visual field was quite narrow. Although the visual quality of the Google Cardboard approach is worst—basically depending on the quality of the used mobile device—it has the highest potential for daily in-field use, e.g. when observing and tracking a flock of birds *in situ*. The downside of current mobile VR solutions are the small screen space preventing multiple views, perspectives, or sophisticated data representations, e.g. of analysis results, and the low graphics and computing power.

4. Discussion

Engaging researchers in a visually immersive environment, while providing direct access to their data with representations of crucial influence factors, is a key advantage of the discussed IA environments. There is a high potential for developing a collaborative platform for bird behaviour analytics. We proposed and investigated different strategies, with a focus on the affordances and requirements of immersive environment designs. These approaches can be further extended to support research and outreach. For collective behaviour research, we are currently exploring the integration of methods for automated data analysis such as network analysis, e.g. to detect and categorize behavioural patterns, and position prediction based on live data streams. For outreach, the approaches could be extended to meet the requirements of museums, with simplified interaction and with a storytelling perspective. Also, further IA approaches and methods such as hybrid 2D and 3D visualizations [49] or distributed collaborative monitor walls [50] could be investigated. A key requirement is that design and implementation suit the needs of the domain experts, where one of our key findings shows that, at least for bird movement analysis, the design space is still restricted by practical constraints (such as fieldwork conditions, computational power and network speed).

Given the speed of advances in technology over recent years, we however conjecture that the immersion in movement data will provide increased efficiency in the workflow of biologists. It will allow them to gain a better overview of the data, recognize specific patterns and formulate hypotheses based on interaction with the data in conjunction with additional contextual information. A further exploration and evaluation of immersive environments for that purpose will be required to characterize the benefits for specific workflows.

Environments that support collaborative analysis, such as the tiled display wall, but also shared virtual environments, allow groups of researchers and data explorers to join forces, with the potential to create new ways of analysing movement data. Ultimately the pace at which data production is increasing will necessitate more efficient ways of interacting with them if we are to transform these data into knowledge.

There have been substantial efforts to raise public awareness for environmental issues, particularly climate change [51] and bird migration patterns [52], and these have been largely implemented on conventional 2D environments such as websites or printed documents. Immersive technology has not been widely adopted as a platform for promoting public awareness, but we foresee a change with the advent of commodity hardware. Studies have also found a high acceptance rate of young audiences for 3D immersive environments, with an additional benefit of having better memory retention [53]. In this work, we have proposed several interesting solutions for public engagement, which can be deployed in public venues to engage the general audience with urgent environmental issues.

Data accessibility. The data used in this work are archived in the Movebank Data Repository [42].

Authors' contributions. K.K. and B.S. drafted and co-authored the manuscript, led the writing and the immersive environment design, supervised the development of the immersive environments, and conducted and evaluated the expert study. K.K. revised and edited the final version of the manuscript. H.N. implemented prototypes of several immersive environments, and contributed to parts of the manuscript. A.F., K.S. and M.N. provided data for testing, expertise on bird movement analysis, and contributed to the environment design, manuscript writing and revision. M.Q., W.F. and M.W. provided data for testing and expertise on bird movement analysis. S.P.F., Y.Z., K.R. and A.G. provided software implementations of immersive environments, and contributed to parts of the manuscript. F.S. co-authored the manuscript, and managed the development of the immersive environments. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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Endnote

[1] See https://www.mapbox.com/.

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