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RESEARCH ARTICLE

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A remote-controlled observatory for behavioural and ecological research: A case study on emperor penguins

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Abstract

1. Long-term photographic recordings of animal populations provide unique insights into ecological and evolutionary processes. However, image acquisition at remote locations under harsh climatic conditions is highly challenging.
2. We present a robust, energetically self-sufficient and remote-controlled observatory designed to operate year-round in the Antarctic at temperatures below −50°C and wind speeds above 150 km/h. The observatory is equipped with multiple overview cameras and a high resolution steerable camera with a telephoto lens for capturing images with high spatial and temporal resolution.
3. Our observatory has been in operation since 2013 to investigate an emperor penguin (*Aptenodytes forsteri*) colony at Atka Bay near the German Neumayer III research station. Data recorded by this observatory give novel biological insights in animal life cycle and demographic trends, but also in collective and individual behaviour. As an example, we present data showing how wind speed and direction influence movements of the entire colony and of individual penguins. We also estimate daily fluctuations in the total number of individuals present at the breeding site.
4. Our results demonstrate that remote-controlled observation systems can bridge the gap between remote sensing, simple time-lapse recording setups, and on-site observations by human investigators to collect unique biological datasets of undisturbed animal populations.

KEYWORDS
animal colony, Antarctica, behaviour, emperor penguin, remote-controlled observatory, time-lapse imaging

1 | INTRODUCTION

The rapid loss of biodiversity linked to the effects of human-induced environmental changes is one of the most important challenges we face today (IPCC, 2014). Polar regions are experiencing particularly rapid and drastic changes, which is alarming as polar species still remain poorly studied due to technical and logistical challenges imposed by the harsh environment and extreme remoteness (Le Bohec, Whittington, & Le Maho, 2013). Developing technologies and tools for monitoring such wildlife populations is, therefore, a matter of urgency.

Continuous data collection over prolonged time periods is the mainstay of ecological and behavioural studies for understanding population trends and group dynamics. Time lapse imaging has become a standard tool due to the availability of digital cameras (Kucera & Barrett, 1993; Lynch, Alderman, & Hobday, 2015; Newbery & Southwell, 2009) as well as the steadily increasing capability of image processing software (Dell et al., 2014; Gerum, Richter, Fabry, & Zitterbart, 2017). Autonomous or remote-controlled observatory networks are becoming increasingly important for the long-term exploration and multi-scale monitoring of ecosystems (Aguzzi et al., 2012, 2015; Danovaro et al., 2017), particularly in remote and climatically harsh locations where data acquisition and physical access to the observation system can be challenging. In this report, we describe the implementation of a remote-controlled and energetically self-sufficient observatory and its application for ecological research.

We designed the observatory with the aim to investigate the population and behavioural ecology of emperor penguins (Zitterbart, Wienecke, Butler, & Fabry, 2011; Zitterbart et al., 2014). We faced a number of challenges: emperor penguin colonies are poorly accessible, and their mating and breeding behaviour can only be observed during the coldest and darkest months, with wind speeds up to 150 km/h and temperatures as low as −50°C. We, therefore, needed a robust, autonomous and/or remotely controlled observation system that requires low maintenance and can withstand the harsh environmental conditions of the Antarctic winter. Furthermore, emperor penguins do not have static breeding places. As they do not build a nest and are incubating their single egg on their feet, the whole colony can move within an area of several km^2, usually on land-fast ice (seasonal sea ice). To observe such a large area, we installed three stationary wide-angle cameras with 3 megapixel (MPx) resolution for a panoramic overview images, and a steerable 11 megapixel camera mounted on a pan-and-tilt unit. This camera is equipped with a telephoto lens for either high-resolution images, stitched panoramic images, or video recordings of the colony.

Our observatory, in the following referred to as SPOT (Single Penguin Observation and Tracking), was deployed in the Austral summer season 2012/2013 to observe the emperor penguin colony at Atka Bay (70°37.0′S, 8°9.4′W), *c.* 8 km north of the German Antarctic research base (Neumayer Station III), on the Ekström shelf ice. Since 2013, we have been collecting wide-angle overview images at a rate of 1 frame per minute to determine the colony position, daily panoramic images stitched from 135 high resolution images to count penguins, and on-demand high-resolution video recordings of the colony at five frames per second (fps).

In the following sections, we describe the design and implementation of the hardware and software, discuss our practical experiences with the system and present data that illustrate the range of possible ecological applications. The observatory has been proven to be robust during extensive field testing in Antarctica, and we therefore expect its design, with minor modifications, to be suitable also in other remote and climatically challenging locations for studying a wide range of species.

2 | MATERIALS AND METHODS

The observatory is based on a 10 ft shipping container mounted on a sledge for ease of transportation and repositioning along the shelf ice edge (Figure 1). The container is used as a platform for mounting components, and as a shelter for maintenance work. All cameras are installed on top of a 6 m high pylon attached to the container (Figure 2b), resulting in a total elevation of the cameras of 20.5 m above sea ice level. The elevated camera position provides a favourable tilt angle, which gives a higher spatial resolution in y-direction but also causes the camera to be more susceptible to wind-induced vibrations.

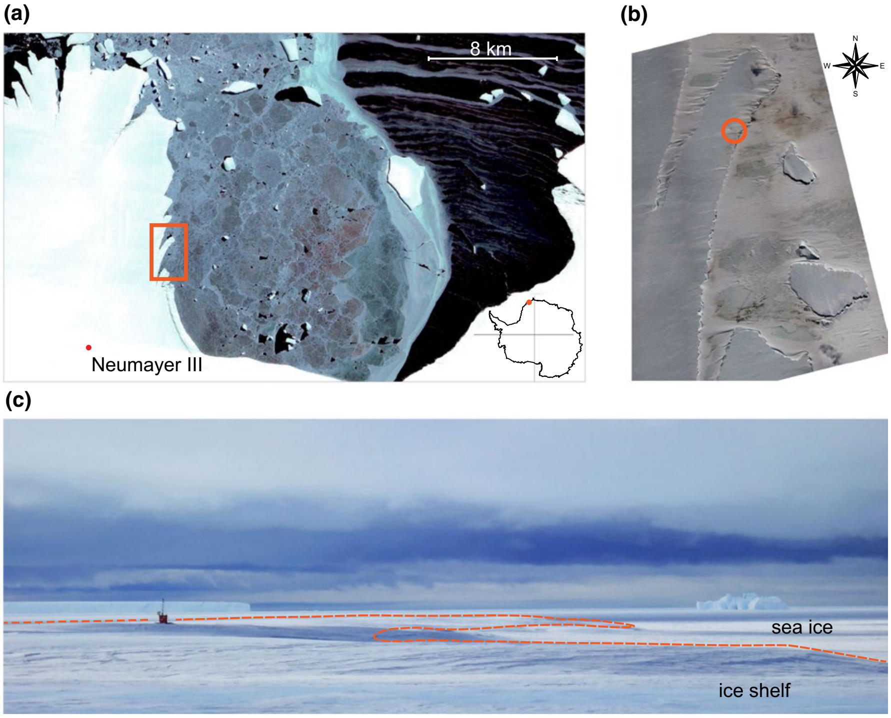

FIGURE 1 Location of the Single Penguin Observation and Tracking (SPOT) observatory. (a) Satellite image of Atka Bay (contains modified Copernicus Sentinel data (2017)). (b) Detailed image of the area (2013). The location of SPOT is indicated by the orange circle; past positions of the penguin colony can be estimated from bird droppings on the sea ice (brown staining). (c) SPOT is positioned close to the edge of the shelf ice (orange dashed line), providing an elevated viewing position over the bay area

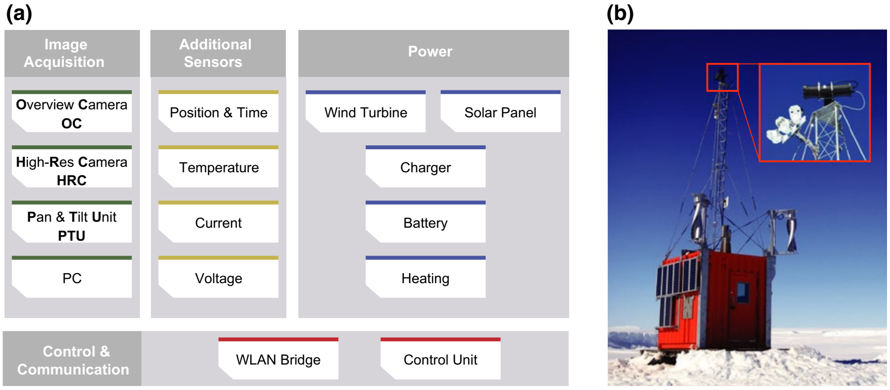

FIGURE 2 Components of the observatory. (a) Component groups of the observatory: image acquisition (green), additional sensors (yellow), power supply (blue), and control & communication (red). (b) Image of the Single Penguin Observation and Tracking (SPOT) observatory. Inset: detailed view of the pan-and-tilt unit, high-resolution camera (black housing), and three overview cameras (white)

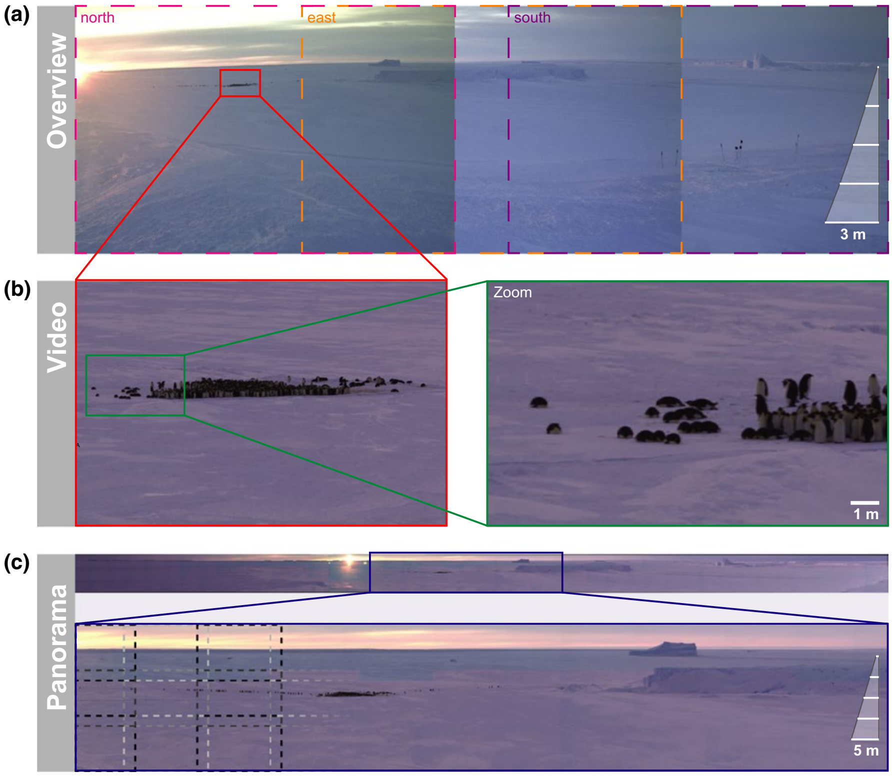

FIGURE 3 Single Penguin Observation and Tracking (SPOT) recording options. (a) Overview image: Three webcams supply an overview over the bay (see Supplementary Files SF1-3). (b) Video mode: A full frame CCD camera with a 400 mm telephoto lens mounted on a pan-and-tilt unit is used to record high-resolution (11 MPx) images or videos at 5 fps. Left: full image (see Supplementary File SF4), right: detail. (c) Panoramic mode: Multiple single high-resolution images are stitched together. Top: panoramic image from 3 rows, 45 columns of high resolution images (see Supplementary File SF4), bottom: detail. Dashed lines indicate the 20% image overlap for seamless stitching

2.1 | Technical implementation

The following sections describe the components of the observatory and their interactions. A detailed list of parts is supplied in the Supplementary Information (Table S1). The components are grouped by tasks (Figure 2): image acquisition, additional sensors, power, and control & communication.

2.1.1 | Image acquisition

Three weatherproof security cameras (M12 D/N, 45° horizontal field-of-view (FOV), Mobotix, Langmeil, Germany) record a wide-angle view of the observed area, at a rate of one image per minute. The cameras are equipped with two different imaging systems, a 3 MPx color sensor and 1 MPx grayscale sensor for low light conditions. The overview images are transmitted to a server in Germany through a WLAN-bridge and satellite transmission (described below in section “Communication”), and are accessible to a remote operator who can then decide if the high-resolution camera should be switched on, and where to point it (Figure 3a). Furthermore, these overview images are valuable for continuous observations of the colony and are therefore stored for later use.

The high-resolution camera (GE4000 C; Allied Vision, Stadtroda, Germany) is mounted on a pan-and-tilt unit (PTU D48E; FLIR, Wilsonville, OR, USA) in a heated and vacuum panel (va-q-vip F, va-q-tec, Würzburg, Germany) insulated camera housing. The pan-and-tilt unit can cover a horizontal FOV of 360°. The camera has a 35 mm full frame CCD image sensor (KAI-11002) for recording 11 MPx color images (4,008 × 2,672) at 5 fps. The camera is equipped with a 400 mm lens (EF 400 mm 1:5.6; Canon, Tokyo, Japan), resulting in a horizontal FOV of 5°, corresponding to a pixel representation of 1 cm at a 1,000 m distance. The aperture and focus of the telephoto lens are electronically controlled with an EF-Mount adaptor (EF-Mount, Birger Engineering, Boston, MA, USA) and can either be manually adjusted by the operator or by an auto-focus/auto-exposure algorithm.

The high-resolution camera can be operated either in video mode or panoramic mode.

In video mode, the camera records images at a fixed, user-defined position at high frame rates (5 fps) and full resolution (11 MPx). The video recordings can be stored as single image files (jpeg, approximately 2 MB per image) or as an H.264 encoded video. Video compression achieves up to 5× smaller file sizes compared to single file jpeg compression but is susceptible to wind-induced vibration artefacts. Therefore, the H.264 encoding mode is only used when the wind speed is below 5 m/s.

In panoramic mode, the camera records images over multiple rows and columns of defined adjacent positions with 20% overlap that can be stitched to a large (*c*. 925 MPx) panoramic image (Figure 3c).

To reduce the required disk space and WLAN transmission time, all pre-processing (flat-field and dark-field corrections, de-mosaicing) and encoding steps (jpeg, H.264) are performed on the observatory's pc (IPC2, fit-pc, i7m, 16GB RAM). The software for image processing is custom-developed and based on the Allied Vision SDK, openCV, ffmpeg, libx264 and libjpeg-turbo libraries. The complete software package currently running on SPOT is available for download.

2.1.2 | Additional sensors

A GPS sensor (GPS 17xHVS, Garmin) is used to monitor the position of the observatory, as the ice shelf is moving with a speed of approximately 100 m per year. In addition, the GPS supplies a precise timestamp for image recordings. Battery voltage, electrical input current (wind, solar) and output current (consumption of the system), as well as the on/off state of all connected components, are measured with a central microcontroller unit (Barionet 100; Barix, Zürich, Switzerland). Temperatures are measured inside the camera housing and inside the box that holds the electronic components. The latter sensor is also used to control the automatic battery heating system.

2.1.3 | Power supply and management

Power is supplied by two wind turbines (WS-0,30 A, Windside, Viitasaari, Finland) and an array of eight solar panels (55 W each, ET-Solar, Nanjing, China). While the solar panels alone are sufficient from spring through autumn, wind turbines are necessary to supply power between May and August (see Figure S1).

Energy is stored by a set of ten absorbent glass mat (AGM) deep cycle batteries (GPL-27T AGM, Lifeline Batteries, San Dimas, USA) with a total capacity of 1,000 Ah. The large capacity allows the observatory to be operated during prolonged periods without sufficient sunlight and wind that can range from days to weeks, depending on the duration of video recordings. Furthermore, the high ratio of total battery capacity to power drain increases battery life time at low temperatures.

An important aspect of energy management is heat conservation and insulation, to reduce low temperature stress on electronic components and to increase accessible battery capacity. Batteries and electronic devices are densely packed in a 1,650 × 750 × 670 mm aluminium box (K470 40 876; Zarges, Weilheim, Germany) to utilize the waste energy for heating. The box is thermally insulated with 20 mm thick vacuum insulated panels (va-q-vip F, va-q-tec, Würzburg, Germany), providing a thermal conductivity of $k < 0.007$ W/(mK). If the batteries are fully charged, excess energy is used to heat the box using resistor mats (24 W, Thermo Technologies, Haute-Savoie, France). The large heat capacity of the batteries in combination with the thermal insulation results in a cooling time constant of approximately 10 days.

To further conserve energy, we implemented three operation modes with different power consumption, ranging from full high-resolution recording mode (high-res 11 MPx images at 5 fps, up to 120 W), overview-only recording mode (3 MPx images from three webcams at one image per minute, 24 W), and an intermittent sleep mode (3 MPx images from three webcams at one image per hour, <6 W).

2.1.4 | Control & communication

Communication between components inside the observatory is implemented via Ethernet (cameras, pc) or RS232 routed over a terminal server (GPS, pan-and-tilt unit). To facilitate remote-controlled operation, a bidirectional exchange of information is necessary for the transmission of control commands, status reports of the observatory, and recorded image data.

We used a WLAN-bridge (PowerStation5; Ubiquiti, San Jose, CA, USA) with transfer rates of up to 2 MB/s to connect to the nearby (8.4 km) Neumayer III station's satellite uplink. Control commands are sent via a server at the station either by a web interface or terminal. The server at Neumayer polls status reports (power levels, temperatures, etc. - see section "Sensors") every minute.

The compressed images are stored on the observatory pc and are asynchronously transmitted to the server at the station where they are automatically stored on hard drives. If the high-resolution camera is running, a highly compressed image (*c*. 30 kB) is also transmitted from the observatory to the station server every 10 s, from where it can be accessed by a remote operator anywhere in the world. This near real-time transmission of live images allows the remote operator to adjust and point the high-resolution camera. Transmission of image and video data from the station server to a server located in Germany is scheduled during low usage time of the stations' satellite connection. We have also successfully tested data transmission directly between the observatory and a server anywhere in the world via a satellite modem through the BGAN satellite network, but this approach is currently limited by high operational costs.

The central controller of the observatory is a microcontroller unit (Barionet 100; Barix, Duebendorf, Switzerland) that handles all low level functions, for example, sending status reports, collecting sensor measurements (temperature, current, voltage), controlling the on/off state of all components, and controlling the heating system. The microcontroller base module has an IO extension (IO12, Barix), which is used to control custom MOSFET-based relays to switch electronic components on and off.

To offer an additional layer of fault protection, the microcontroller sends every second a heartbeat signal to a hardware watchdog timer relay (MFZ12DDX, Eltako, Fellbach, Germany). Should the microcontroller unit crash and therefore stop sending the heartbeat signal, the timer will initiate an automatic hard reset after 30 s.

3 | RESULTS

In the following sections, we present examples to illustrate how the SPOT observatory is used to address ecological questions. First, we investigate the phenology and abundance of penguins in the Atka colony using high resolution stitched panorama images. Second, we address ecologically driven behaviour of the colony in response to changing environmental conditions. In particular, we study how the colony moves in response to wind speed and wind direction, and how the movement of the whole colony emerges from the movement of individual penguins.

3.1 | Abundance and arrival pattern

For species that live in remote areas, even basic population ecological parameters, such as phenology and abundance, are difficult to assess. Most of our phenological understanding about emperor penguins comes from a single colony near the Dumont d'Urville station at Pointe Géologie (66°40′S, 140°01′E), where researchers have been conducting year-round observations of the animals for decades (from Prévost 1961 to Cristofari et al., 2016). All other emperor penguin colonies are difficult to reach on a regular basis during the winter season; therefore, precise information on the timing of the breeding cycle in most other colonies is lacking. Similarly, accurate population numbers are difficult to obtain as colonies can spread over a wide area (Wienecke, 2010). Remote (satellite) sensing methods, while providing the bulk of Antarctica-wide abundance estimates so far, need frequent calibration across several colonies to correct for fluctuating percentages of animals that are present at the colony site and for fluctuating animal densities, which in turn depends sensitively on environmental conditions (Ancel et al., 2014). Therefore, we explore whether overview and panoramic images recorded by SPOT can be used for reliable arrival date and abundance estimates.

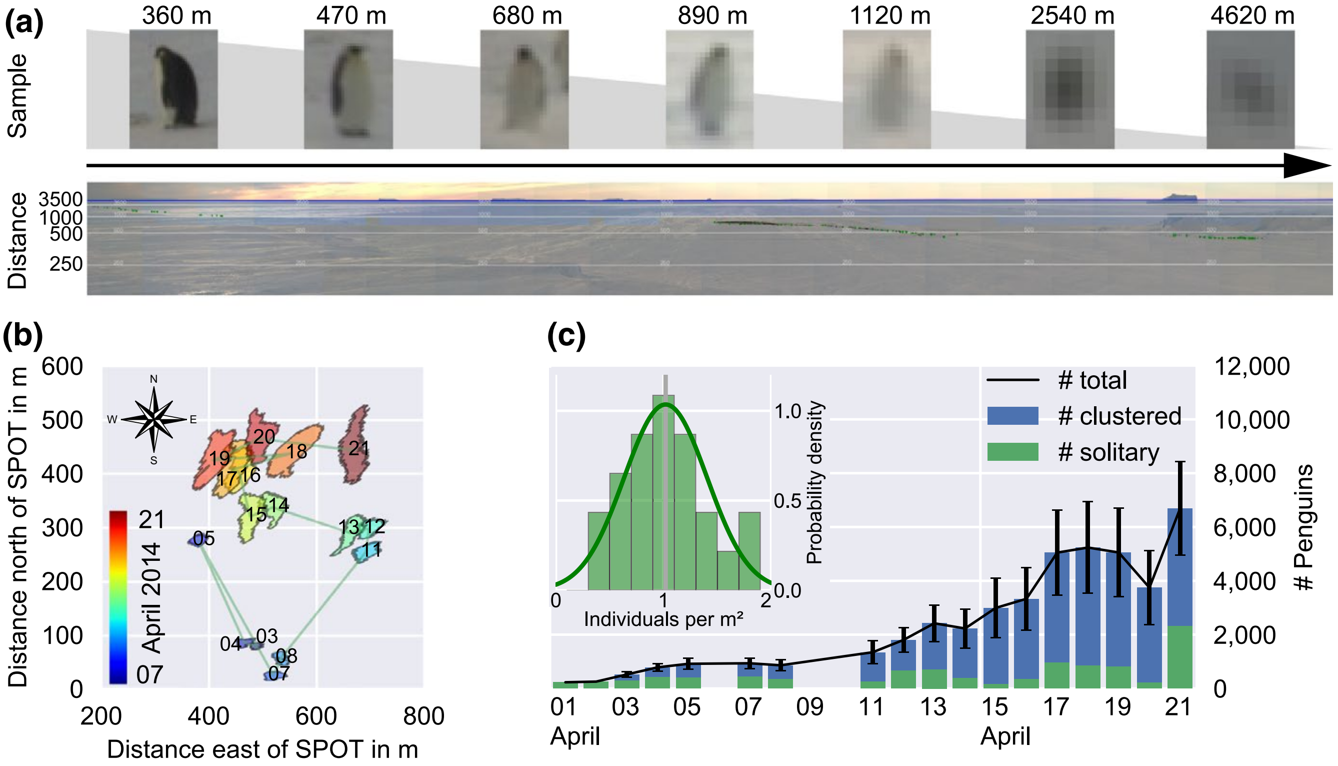

FIGURE 4 Evaluation of emperor penguin numbers and arrival times. (a) Image quality of single penguins at increasing distances from Single Penguin Observation and Tracking (SPOT). (b) Position of the colony during April 2014. (c) Total number of individuals present over time (black), estimated by the sum of solitary penguins (green) and area/density estimates for densely clustered animals (blue) that could not be individually counted. Errors are estimated based on the uncertainty in the projected group area and the variance in group density (inset). The density distribution sampled over 8 days shows an average of 1.01 individuals per m^2

As a proof of concept, we analysed 21 panoramic images recorded in April 2014. Solitary penguins can be reliably identified up to distances of 4 km (Figure 4a) and are manually counted using the ClickPoints image analysis tool (Gerum et al., 2017). Counting penguins in clusters farther away than 600 m, however, is more challenging as individual penguins are not easily distinguishable due to mutual occlusion. To circumvent this problem, we manually marked individual penguins in clusters that are close to the observatory (<600 m, 24 clusters from eight different days with good visibility, see Figure S4) to obtain a distribution of penguin density (Figure 4c inset). As some penguins may also have been obstructed by others in these nearby clusters, we caution that the true density may be somewhat higher (see Figure S4 for representative images). We further assume that the cluster density did not fluctuate over time. We then estimate the number of penguins by multiplying the projected area of the cluster with the average cluster density of 1.01 penguins per m^2 (Figure 4b). The projected cluster area is computed (as described in section "Colony Locomotion" and in Figure S5) from the cluster contour based on the penguin head positions (see Figure S3). The manual labelling of the cluster contour with a ±2 pixel inaccuracy, together with the variability in cluster density as discussed above, gives rise to a total uncertainty of 30% for the total number of penguins present at Atka Bay. Also, being limited to one viewing position, we cannot prevent occlusion of some penguins by icebergs or shelf ice.

Despite these limitations, our capability to take repeated measurements on consecutive days allows us to achieve reliable results. An example is shown in Figure 4c: In 2014, the arrival of emperor penguins at Atka Bay started at the beginning of April, reaching a total of up to 7,000 individuals by April 21, after which we could no longer record due to poor visibility caused by a storm. This number is comparable to estimates of 9,657 individuals based on VHR (very high resolution) satellite images taken in August 2009 (Fretwell et al., 2012). As visual ground counts by human observers are not available at Atka Bay, we re-counted the colony based on a panoramic image taken in September 2017 when the colony was close to the shelf so that nearly every single penguin could be clearly marked. We counted 10,833 adult penguins. Although penguin counts from different seasons cannot be compared without knowing the fraction of penguins that are present at the colony site, these counts suggest that the Atka Bay colony has been stable since 2009. More frequent and regular counts across different seasons and years based on panoramic images will be crucial to monitor the stability of the penguin colony and to facilitate the calibration of satellite-based estimates (Ancel et al., 2014). In our experience, abundance estimates based on panoramic images are an efficient and inexpensive alternative to on-site counting by human observers (Le Maho et al., 2014) or counting based on satellite images (Fretwell et al., 2012).

3.2 | Colony locomotion in response to wind speed and direction

Adult emperor penguins have no inland predators during breeding (Prévost 1961). Their behaviour is largely dictated by weather conditions and the drive to minimize energy loss to ensure successful breeding. Our knowledge about the emperor penguins' behavioural ecology, however, is again predominantly based on data from the Pointe Géologie colony (Ancel, Beaulieu, Le Maho, & Gilbert, 2009; Ancel, Visser, Handrich, Masman, & Maho, 1997; Gilbert, Robertson, Le Maho, Naito, & Ancel, 2006). Detailed knowledge about colony-specific or location-specific behavioural traits is largely missing (but see Zitterbart et al., 2011, 2014). In this section, we present how low and high resolution images acquired with SPOT are used to investigate the behaviour of individual penguins and of the colony as a whole in response to wind speed and wind direction.

Over the last years, several colonies have been reported to occasionally move their breeding location from the sea ice to the shelf ice (Fretwell, Trathan, Wienecke, & Kooyman, 2014; Zitterbart et al., 2014). It is debated, however, whether this behaviour is an adaption to thinning sea ice conditions (Fretwell et al., 2014) or, alternatively, whether it is simply caused by exceptional meteorological conditions, such as strong onshore winds in combination with snow drift that made the shelf ice accessible (Zitterbart et al., 2014). Indeed, it has been reported that emperor penguin colonies move with the dominant wind direction (Le Maho, 1977), and computer models suggest that wind is a driving factor for the locomotion of huddling emperor penguins (Waters, Blanchette, & Kim, 2012). However, a quantitative experimental analysis of colony movements in response to the extreme wind conditions found throughout Antarctica, including strong winds and rapidly changing wind direction, has thus far not been performed.

Using data from continuous overview recordings (overview camera, 3 MPx) spanning five consecutive days in April 2013 with good visibility (Figure 5a), we correlate wind direction and colony movement direction. Despite their low resolution, overview images provide continuous recordings over an area of 9 km^2 of Atka Bay, and are therefore well suited to monitor large-scale colony movements. The colony position is manually segmented from 18 selected images, each taken at least 3 hr apart (Figure 5b), which properly resembles the full distribution of environmental conditions encountered during the five consecutive days (Figure 5d). A top-view projection of the colony area (Figure 5c) is then computed based on distance calculations using the visible horizon in the image as a reference, and taking the camera FOV and camera elevation into consideration (Figure S5). The camera bearing is calculated based on the GPS position of the observatory in combination with a distinct landmark with known GPS coordinates (iceberg on the right side of Figure 5a). The projected colony area increased during the observation period as additional penguins were continuously arriving at the colony site (Figure 5c). We calculate the colony's displacement and heading based on the centre of mass of the projected area. Wind speed and direction are measured in 1 min intervals and are averaged over the 3 hr preceding the image acquisition.

Our results show that the direction of colony locomotion closely follows the wind direction (Figure 5c), with a statistically significant ($p < .05$) correlation of $r = .60$ (Figure 5d). The correlation r is defined as:

$$r = 1 - \frac{|(\alpha_{\text{wind}} - \alpha_{\text{colony}})|}{90^{\circ}}$$

resulting in $r = 1$ for parallel and $r = -1$ for antiparallel movement vectors. During periods with wind speeds above 5 m/s, the correlation

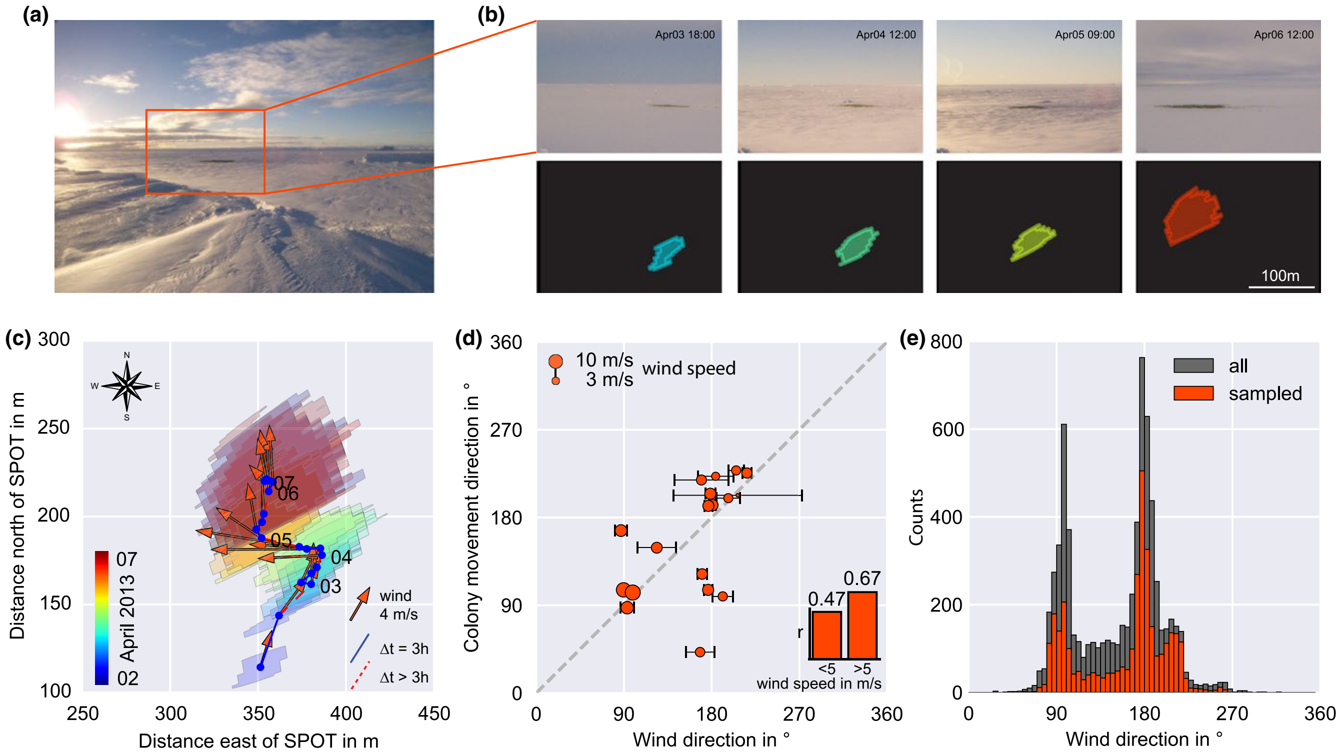

FIGURE 5 Influence of wind speed and wind direction on the position of the Atka Bay emperor penguin colony. (a) Image of the colony taken by one of the overview cameras. (b) Colony position over time (upper row) and corresponding segmented and projected area (lower row). (c) Colony projected area over 5 days (from blue to red), centre of mass positions (blue circles) are shown with the corresponding wind direction (red arrows) and speed (depicted by arrow length). (d) Direction of colony movement relative to wind direction (direction is defined clockwise relative to north (0°)). Wind speed and direction are averaged over the last 3 hr preceding the image acquisition. Wind speed magnitude is depicted by the marker size. (e) Distribution of wind directions in the sampled sequences (16 × 3 h, orange bars) compared to the whole period (02 April to 07 April 2013, grey bars)

between wind and colony movement direction increases to 0.67, but even for wind speeds below 5 m/s, the correlation remains substantial with *r* = .47 (Figure 5d inset). This observation is striking, given that the metabolic rate of emperor penguins is not affected by wind speeds below 5 m/s (Le Maho, 1977). Taken together, our findings support the notion that occasional shelf ice visits of the colony (Fretwell et al., 2012; Zitterbart et al., 2014) are not a response to thinning sea ice conditions, but are the result of wind-induced colony movements.

The locomotion of the whole colony is necessarily driven by the locomotion of individual penguins, which we can extract from high-resolution video recordings. Our image quality is sufficient to observe solitary penguins over distances of up to 4 km, and to track the movements of individual penguins in huddles or clustered groups over distances of up to 600 m, depending on weather and light conditions.

In the following example, we analyse single-penguin locomotion of a huddle located at a distance of 400 m to 440 m from the observatory. The huddle is facing wind speeds of up to 12 m/s from a north-eastern direction (Figure 6a). Wind induced camera shake is removed by a template-based stabilization algorithm (Gerum et al., 2017; see Supplementary File SF6). Multiple individual penguins moving on the windward and leeward side of the colony are tracked manually for up to 60 s.

We find that penguins at the wind-protected leeward side of the huddle move along the colony border in random directions and with different velocities. By contrast, penguins on the wind-exposed windward side move predominantly in the downwind direction and with similar velocities (Figure 6b,c and Supplementary File SF6), which we attribute to a single-file movement pattern. In addition, the average speed of moving penguins at the windward side of the huddle is significantly (*p* = .026, one sided Mann–Whitney *U* test) lower compared to moving penguins at the leeward side. The net effect of the slower but more persistent downwind movement of the penguins from the windward side to the leeward side is a slow downwind movement of the entire group. This mechanism therefore explains our finding of a tight correlation between wind direction and colony locomotion as described in the previous section.

The temporal resolution of the video recording mode (5 fps) allows for a detailed description of the movement characteristics. From the velocity fluctuations of a moving penguin over time, we can extract the step duration, as illustrated in Figure 6d. These velocity fluctuations are not caused by residual camera movements, as penguin tracks at the windward and leeward side, when recorded at the same time (Figure 6d), show no correlation. Interestingly, the distributions of step durations (Figure 6e) for penguins at the windward versus leeward side are indistinguishable (*p* = .7, Kolmogorov–Smirnov test), indicating that the observed differences in the speed of penguins moving along the windward versus leeward edge (Figure 6c) are attributable

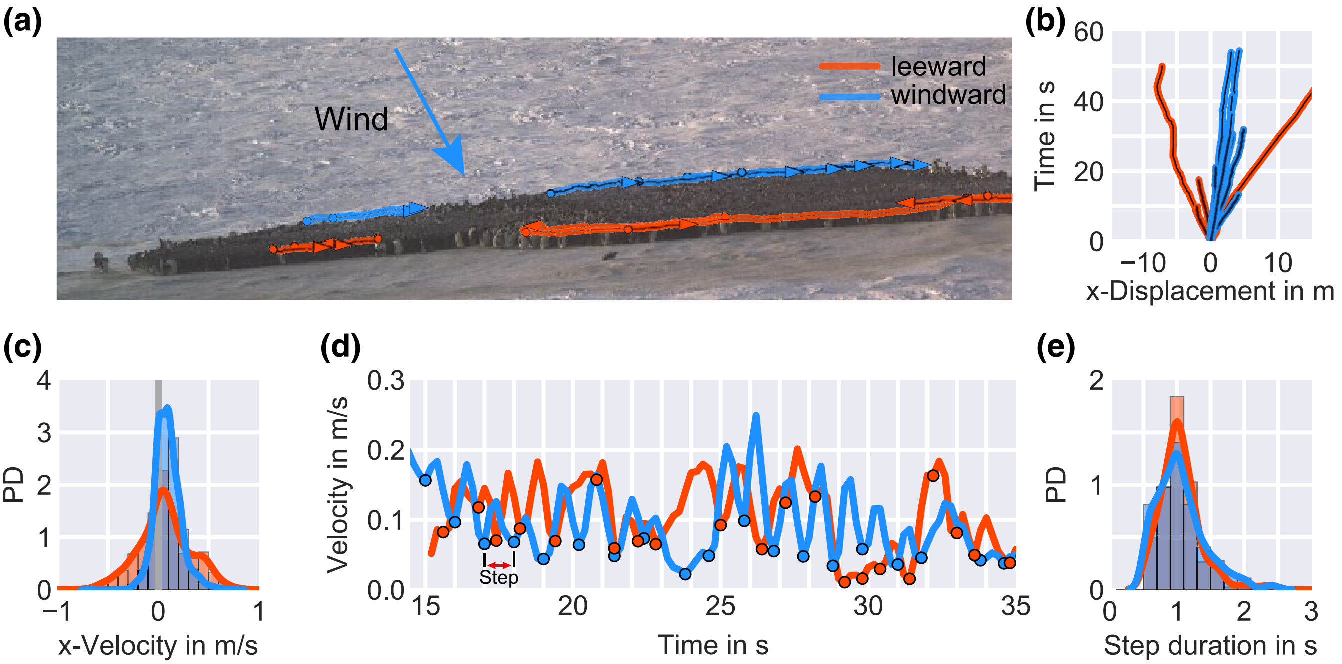

FIGURE 6 Movement characteristics of single emperor penguins at the huddle boundaries. (a) Penguin tracks on the windward (blue arrows) and leeward (red arrows) side of the huddle (see Supplementary File SF6). The dominant wind direction is marked by the straight blue arrow. (b) Representative penguin displacements relative to starting position. (c) Distribution of penguin displacement velocities in *x* direction. Windward side penguins move persistently in one direction and share similar speeds, in contrast to leeward side penguins that move randomly in both directions and with different velocities. (d) Velocity magnitude fluctuations of two representative penguins over time. The intervals between minima (marked by circles) are interpreted as step durations. (e) Distribution (probability density) of step durations for penguins on the windward (blue) versus leeward (red) side. Despite their different movement velocities, penguins on the windward and leeward side both exhibit the same average step frequency of 1 Hz

not to different step frequencies but step lengths. This finding is counter to the intuitive assumption that penguins in a queue wait for a sufficient gap to appear in front of them before they move. A similar behaviour has been reported for humans in dense queues, who are reluctant to stand still and instead prefer to perform small steps (Jelić, Appert-Rolland, Lemercier, & Pettré, 2012).

4 | DISCUSSION

4.1 | Feasibility

The SPOT system is a customizable and reliable observatory able to operate in remote and climatically hostile locations for long time periods without on-site user intervention. SPOT has been tested with success in Antarctica, where it has been in operation since January 2013. Since then, we have continuously improved the hardware and software of the observatory. We learned that the H.264 video compression results in excessive vibration artefacts when wind speeds exceed 10 m/s, therefore we now save the video stream as single jpeg-compressed full frame images at higher wind speeds. Moreover, the original thermal insulation of the camera housing with polyurethane open-cell foam was hydroscopic and released water at low temperatures, which in turn caused water condensation at the front window of the camera housing, which is naturally the coolest part. We have therefore replaced the thermal insulation with vacuum insulated panels, and replaced the front window with an Indium-Tin-Oxide (ITO) coated borosilicate glass plate (thickness 1.2 mm, diameter 86 mm). The ITO coating has an electrical area resistance of 4 Ohm per square, and with a total heating current of 0.3 A, defogging can usually be achieved within <5 min (Figure S2).

The wind turbines need to be re-greased every 3 months, depending on weather conditions, but no further regular service or maintenance is required. Power supply and data storage worked without flaws, with one exception in 2015 when both wind turbines (rated up to 200 km/h) were damaged during a storm. Despite the use of consumer-grade components and exposed moving mechanical parts for the camera, our experience confirms that the observatory can be operated in Antarctica during the entire winter without the support of nearby technicians.

4.2 | Comparison with other methods

Given the short distance of 8 km between the Atka penguin colony and the Neumayer III station, it could be argued that video observation could have been possible also with the help of a human observer. Our experience refutes this notion. During deep winter, a visit always requires a team of two, and at least 3 hr for preparation and driving, in addition to the time spent recording. Due to the frequently poor visibility, occasionally far distances between the colony and the edge of the shelf ice, and limited outdoor time due to low temperatures, the total video footage obtainable with the help of a human observer is therefore severely limited. By comparison, the total video footage from SPOT averages 60 hr per winter season, not including the round-the-clock recordings from our overview cameras. SPOT has also the advantage to be less dependent on logistical constraints (e.g. access, travel costs, accommodation) compared to a human observer, and in the long run is far more cost efficient. Moreover, while SPOT is considerably more complex than pure autonomous time-lapse systems (Newbery & Southwell, 2009) or camera traps (Kucera & Barrett, 1993), it is capable of gathering high-resolution images with much higher temporal resolution and on-demand recordings. Combining overview and high-resolution steerable cameras allows us to record images over various temporal and spatial scales. Finally, because the observatory is mobile (it is mounted on a sled), it can be easily relocated to a different position, which is in our case necessary every second year due to the moving ice shelf.

A useful feature of a steerable tele-lens camera is the ability to record high-resolution panoramic images on an hourly to daily basis to estimate the number of individuals present at the site. Compared to aerial or satellite-based systems that have become a viable option for abundance estimates of animal colonies (see Trathan, 2004 and Fretwell et al., 2012 for penguins, LaRue et al., 2011 for seals), panoramic images offer the advantage that the animals can be counted regardless of cloud cover, and at a much lower cost. Compared to on-site manual counting, the penguin colony is not disturbed by the presence of human observers that could potentially cause stress to the animals and bias the recorded data (Le Maho et al., 2014).

4.3 | Practical application and system adaptability

The modular hardware and software architecture of the SPOT observatory has allowed us over the past years to upgrade the observatory with ease. For example, during the summer season 2016/2017, we have installed four additional overview cameras to increase the observable range to 300°. We have also upgraded the high-resolution camera with a 29 MPx model (GX6600C, Allied Vision). Other sensor extensions that are similarly straight-forward to implement may include multispectral cameras with infra-red capability for conducting metabolism studies, or directional acoustics sensors for investigating the soundscape of the colony. Consequently, the design of the observatory can be easily adapted to other tasks where a remote-controlled observation platform is required to withstand harsh environmental conditions, to observe colonies or groups of animals with high mobility but a fixed local attraction point, for example, a seabird breeding ground, a beach with seals, or animals returning to a water hole.

In less demanding environments, the observatory can be greatly simplified. A protective 10 ft. container may not be necessary, and since the electronic components of the system fit into a Zarges box, only a sturdy tripod or pylon for the camera needs to be erected. Also, no thermal insulation may be required. If enough daylight is available to power the observatory solely with the help of solar panels, wind turbines and an excessively large battery pack become obsolete. In addition, with more available light, a smaller camera and zoom lens with a lower light efficiency become feasible, for which a smaller and less powerful pan and tilt unit can be used. Such a down-sized system would be considerably less expensive and also small and light-weight enough to carry, for example, in mountainous areas or, if the terrain permits, to be mounted on a rover or similarly mobile platform to increase the observation range.

4.4 | Relevance and perspective in ecology and evolution

Due to its highly customizable design, the SPOT observatory has a wide range of applications. From the continuous time series of overview and high-resolution images, classical population and phenology parameters can be easily extracted, such as arrival date for breeding, laying, hatching and fledging, as well as the annual breeding success, population size, or the proportion of individuals in a specific state. Previous studies that would have benefited from such continuous time series include studies in bird colonies, such as thick-billed murres *Uria lomvia* (Merkel et al., 2014), lesser flamingos *Phoeniconaias minor* (Kaggwa, Gruber, Oduor, & Schagerl, 2013) and cape gannets *Morus capensis* (Mullers & Navarro, 2010). Continuous biological time series, in particular those that span over several years or decades, are scarce but are critical for population modelling to evaluate current and future trends, and to estimate the adaptive capacities of a species to cope with natural and anthropogenic environmental changes. As an added benefit, SPOT allows data collection without disturbances from human observers and without subjective bias. Moreover, SPOT enables us to study dynamic processes and emerging collective properties such as physical organization and collective movements in groups of animals (Berdahl, Torney, Ioannou, Faria, & Couzin, 2013; Gerum et al., 2013; Hein et al., 2015; Zitterbart et al., 2011) by means of visual tracking (Dell et al., 2014) and identification (Kumar & Singh 2017).

Over the expected multi-decade life-time of the observatory, we will be able to monitor how short-term and long-term environmental changes affect the Atka-Bay emperor penguin colony. The Atka Bay colony (as all other Dronning-Maud-Land colonies) is predicted to be severely affected by climate change and, as one of the first colonies, to disappear completely (Jenouvrier, Garnier, Patout, & Desvillettes, 2017). With low-cost global high-speed satellite Internet in reach within the next years, we aim to distribute several SPOT observatories at different emperor penguin colonies along the Antarctic coastline and build a network of ecological observatories that fits into the framework of the Scientific Committee of Antarctic Research program. Implementing cost-effective continuous monitoring will help to validate model predictions of the emperor penguins' fate, and to facilitate informed decisions regarding the species' IUCN Red List of Threatened Species status.

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AUTHORS' CONTRIBUTION

D.Z. and B.F. conceived the experiments. S.R., W.S., B.F. and D.Z. developed and built the observatory, S.R. and R.G. analysed the data. S.R., R.G., B.F., C.L.B. and D.Z. wrote the manuscript.

DATA ACCESSIBILITY

All data used in this article are publically available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.19ph7 (Richter et al., 2018). The SPOT software package is available for download at: http://bitbucket.org/fabry_biophysics/mee_spot_software.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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