

RESEARCH ARTICLE

Global positioning with animal-borne pressure sensors

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Funding information

Bundesamt für Umwelt, Grant/Award

Number: 254, 332, 363 and 400;

Schweizerischer Nationalfonds zur

Förderung der Wissenschaftlichen

Forschung, Grant/Award Number: 191138

Handling Editor: Emily Shepard

Abstract

1. Over the past decades, tracking technologies have become more ubiquitous and helped uncover crucial spatiotemporal relationships in nature. In order to apply these technologies to small animals and reduce any potential adverse impact of devices, geopositioning methodologies compatible with lightweight devices are highly sought after. Measured by lightweight geolocators, atmospheric pressure provides an untapped opportunity for global geopositioning, as its natural temporal variation is unique to each location.
2. In this study, we estimate the position of birds by comparing pressure data recorded by the geocator with reference data from a global weather reanalysis database. The method produces a likelihood map of the position based on (1) a mask of the locations for which the ground-level elevation matches the pressure measured by the geocator and (2) a mismatch between the temporal time series measured by the geocator and the reanalysis dataset. This new method is introduced step by step and applied to 16 tracks of nine long- and short-distance migrant species.
3. Using known positions of double-tagged individuals (light and pressure data), we demonstrate that our method is almost three times more accurate than light-based positioning with an average error of 44km in our trials. In contrast to the traditional light-based approach, pressure geolocation can provide useful information for short stationary periods (less than a day) and is not affected by the equinox problem nor by any shading effects due to weather or animal behaviour. To facilitate the application of the method, we developed an R package [GeoPressureR](#), together with a user guide [GeopressureManual](#) and starting code [GeoPressureTemplate](#).
4. The use of pressure sensors to position animals has the potential to become widespread thanks to the combination of both affordable lightweight devices (<0.4 g) and this method to estimate position of the device precisely and accurately. In particular, such devices can now be applied to short-distant migrants (>100km), forest-dwelling species, nocturnal animals and altitudinal migrants.

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KEYWORDS

animal tracking, archival tag, archival tags, bird, biologist, ERA5, geolocation, geolocator, lightweight, logger, migration, movement ecology, reanalysis data

1 | INTRODUCTION

Understanding ecological relationships in nature relies on a fine-scale knowledge of the successive positions of individual animals in relation to specific habitats (Sanderson, 1966). To this end, the remote tracking of wild animals has become an important tool in field ecology (Hussey et al., 2015; Katzner & Arlettaz, 2020; Kays et al., 2015). For birds in particular, tracking technologies have revealed long-standing secrets about their whereabouts and migration patterns (e.g. Bayly et al., 2020; Robinson et al., 2010; Shamoun-Baranes et al., 2017).

The past decades have seen general progress of all tracking technologies towards more precision and lighter weight; however, there still exists a trade-off between tracking accuracy and device weight (Bridge et al., 2011). Though the exact nature and extent of the effect of geolocators on tracked animals is still being discussed, there is a consensus that devices should be as light as possible (Bodey et al., 2018; Brlik et al., 2020). Indeed, lighter-weight devices would allow to equip smaller species, but also, most importantly, help reduce any potential adverse effect on equipped animals (Portugal & White, 2018).

Among lightweight technologies (<5 g), archival GPS (Fraser et al., 2017; Hallworth & Marra, 2015; Musseau et al., 2021) and automated telemetry technologies (Taylor et al., 2017) provide the most accurate position, but as the number of estimated positions is often limited, such technologies offer only a coarse-level understanding of migratory movements, with no information on short stopovers.

Light-level geolocators constitute the most affordable alternative lightweight tracking solution (Hill & Braun, 2001; Lisovski et al., 2020; Lisovski & Hahn, 2012). These devices estimate the position of the animal based on the twilight derived from ambient light measurements and the astronomical equation (Hill, 1994; Hill & Braun, 2001). However, these measurements come with large uncertainty (Fudickar et al., 2012; Lisovski et al., 2012, 2018; Porter & Smith, 2013). Indeed, the precision of the method varies greatly with latitude (e.g. no sunrise/sunset at the poles) and time (e.g. same day duration everywhere at the equinox; Hill, 1994). In addition, temporary shading due, for instance, to weather or a change in the bird's behaviour, results in error in the estimated position. Calibration at known locations can help to reduce this error and estimate the associated uncertainty; however, it is specific to the persistent shading at the known location and, therefore, might not hold for other locations. As a result, light-level geolocators provide (1) potentially biased estimates for long stationary periods where no calibration can be done and (2) location estimates with large uncertainty for short-duration stopovers (<2 weeks) or around equinoxes (ca. $\pm$ 2 weeks),

when most migrants are en route. The short stopovers and those around equinoxes are, therefore, often overlooked even though they are crucial to better understand movement dynamics and migration strategies (Philip, 2004).

More recently, multisensor geolocators have expanded the field of research by measuring movement (accelerometer), temperature and atmospheric pressure, in addition to light (Liechti et al., 2018). Accelerometer and pressure data can be used to determine when and how long a bird was in movement (e.g. Dhanjal-Adams et al., 2022). This information helps to improve the position estimate of the light-level geolocator in two ways. First, all twilights occurring during the known stationary periods can be combined to estimate a single location. Second, assuming a distribution of bird ground speed, the duration of flight can be converted into a distance and can ultimately help constrain consecutive positions through a movement model (e.g. Rakhimberdiev et al., 2015; Sumner et al., 2009). Until now, data collected by the pressure sensor (also called barometer or pressure transducer) were used to determine flight altitude and climb rates (Dhanjal-Adams et al., 2018; Dreelin et al., 2018; Meier et al., 2018; Sjöberg et al., 2018), but its potential to improve geopositioning has not yet been exploited.

Atmospheric pressure is related to the force applied by the mass of air above and thus strongly varies with altitude. It is also affected by air density, temperature and humidity, and therefore shows complex spatial and temporal variation influenced by weather, wind, planetary rotation, sun heat and moon gravitation. All these factors contribute to creating a unique time series for each location around the world.

In this study, we present a new method relying on matching the pressure time series recorded by the animal-borne geolocator with an existing spatiotemporal dataset of ground-level pressure reanalysis. We estimate possible positions for each stationary period by (1) matching the pressure time series measured by the geolocator with the reanalysis data and (2) filtering out locations where the elevation does not match the absolute pressure values measured by the geolocator.

This approach is independent of light-level geolocation and can work with pressure sensors alone. In the following, we refer to a geolocator as any device measuring light and/or pressure, while a light-level geolocator refers to a geolocator measuring light only.

2 | MATERIALS AND METHODS

In this section, we briefly present the geolocator dataset (Section 2.1) and describe the steps followed to derive stationary periods, which are required for the method (Section 2.2). We then introduce the method used to estimate the geolocator position based on

pressure data (Section 2.3). Finally, we outline the method followed to estimate position from light data (Section 2.4) to compare positions based on light and pressure.

2.1 | Geolocator data

To test our method with a diverse range of migrants, we use multi-sensor geolocator data from 16 tracks of nine species. The dataset includes four Afro-palearctic migrants, two Palearctic migrants and three Afro-tropical migrants (Figure 1). These species exhibit a wide range of migration strategies in terms of distance covered (664–7192 km), migration duration (5–222 days and 39–474 h of flight) and number of stopovers (9–151). They are all flapping migrants, mostly nocturnal, with some whose flights extend into the day (e.g. Tawny Pipit; Briedis et al., 2020). We included a fully mountainous species (Ring Ouzel; Barras et al., 2021) as well as a seasonal mountainous species (Eurasian Hoopoe; breeding season only) to illustrate the steps required to overcome the challenges raised by altitudinal movement.

All individuals were equipped with SOI-GDL3 PAM devices weighing between 1.3 and 1.5 g (Liechti et al., 2018). The data of interest recorded are as follows: (1) light measured every 5 minutes, (2) activity as the sum of the difference in acceleration on the z-axis of 32 measurements taken at 10 Hz (~3 s) every 5 min and (3) atmospheric pressure (hPa) measured at 5-, 15- or 30-min intervals depending on the geolocator setting.

The dataset essentially represents double-tagged individuals where light and pressure data can be used independently for geopositioning. This enables us to compare the accuracy of the pressure-based geolocation method presented here with light-based geolocation.

2.2 | Identification of stationary periods

A preliminary step required for light- and pressure-based global positioning is to identify periods when the bird has stayed at the same location (km scale) hereafter called stationary period. Different methods can be applied to achieve this step depending on the migration of the species and data available (e.g. Dhanjal-Adams et al., 2022).

Here, as accelerometer data with higher temporal resolution than pressure were available, we determined stationary periods by identifying migratory flights from both continuous high activity data and change in pressure data. Because pressure analysis requires a high precision of classification, we manually label the activity and pressure data using TRAINSET (Kapoor et al., 2021). To accelerate the process, we initialise the labelling with an automatic classification of activity following Dhanjal-Adams et al., (2022). Detailed guidelines, examples and tips on this labelling process can be found in the GeoPressure Manual at <https://raphaelnussbaumer.com/GeoPressureManual/labelling-tracks>.

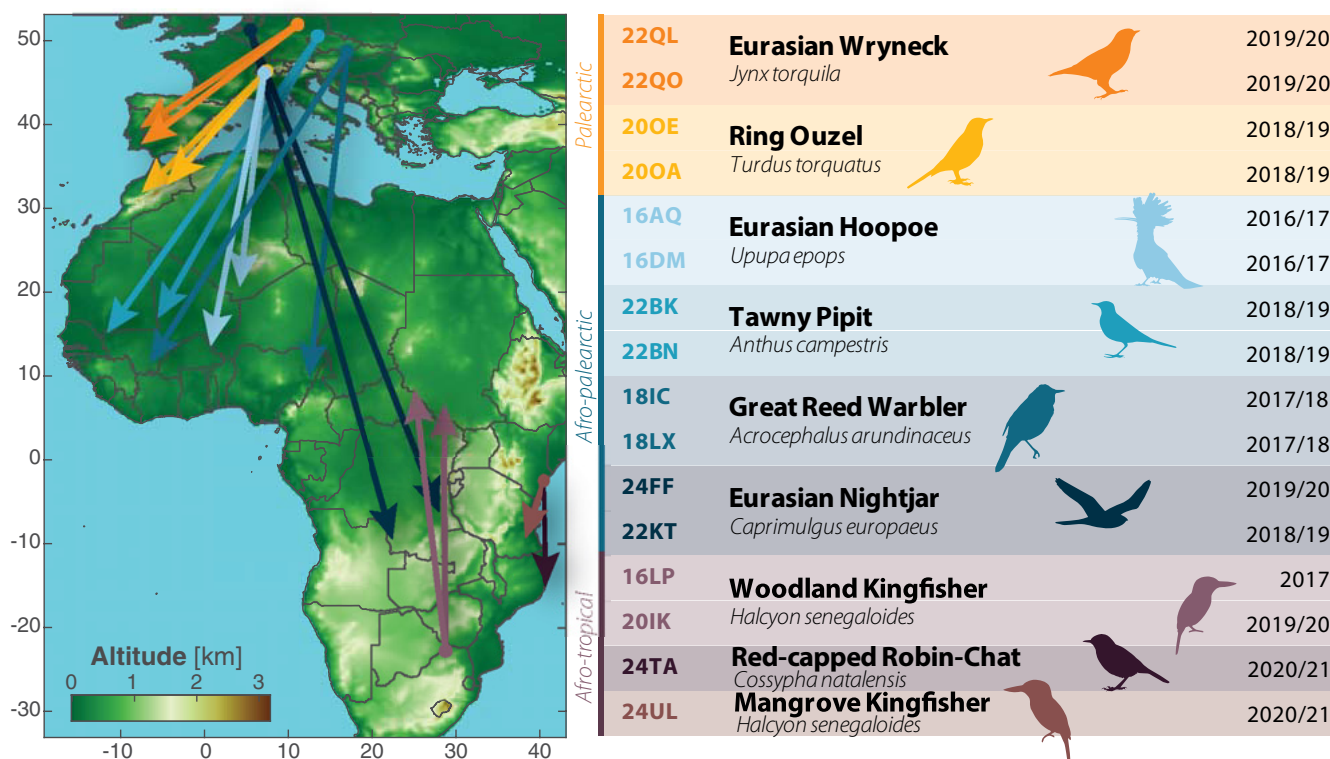


FIGURE 1 Summary of the 16 tracks used in this study illustrating the broad spatial and temporal scope of the dataset. More detail on species-specific migratory patterns can be found in Barras et al. (2021) for the Ring Ouzel, Briedis et al. (2020) for the Tawny Pipit, Emmenegger et al. (2021) for the Great Reed Warbler and Evens et al. (2017) for the Eurasian Nightjar.

Note that this step can be achieved using pressure measurements alone, such that this method can be used with geolocators that measure only atmospheric pressure (e.g. Rhyne & Nussbaumer, 2022; Rime & Nussbaumer, 2022).

2.3 | Creation of position maps from pressure data

For each stationary period, we produce a likelihood map of the bird's position by finding the best match between the pressure time series measured by the geolocator and a weather reanalysis dataset.

In this study, we extract pressure data from the ERA5 surface-level dataset at the maximum available resolution of 0.25° and 1h (Hersbach et al., 2018). To be able to compare the geolocator and the reanalysis time series, we down scale the geolocator pressure to 1h resolution. Beforehand, we remove potential outliers with a moving median of ± 1 datapoint (corresponding to 5, 15 or 30 min depending on the measurement resolution) for each stationary period separately.

The likelihood map is estimated for each stationary period by combining two sets of information: (1) a mask of possible locations for which the elevation matches the absolute value of pressure measured by the geolocator (Section 2.3.1) and (2) the likelihood of the mismatch between the temporal time series measured by the geolocator and the reanalysis data (Section 2.3.2).

2.3.1 | Filtering locations based on absolute pressure values

In this step, we leverage the relationship between pressure and elevation to filter out locations where the pressure recorded by the geolocator does not correspond to the ERA5 pressure at ground level. In summary, this is done by computing the geolocator altitude for each stationary period based on the pressure measurement and comparing this elevation with a digital elevation model.

The ground-level elevation of the reanalysis z_{ERA5} can be computed based on the geopotential Φ ($m^2 s^{-2}$) value provided by ERA5 with

$$z_{ERA5} = \frac{1}{g} \frac{r\Phi}{r - \Phi}. \quad (1)$$

where the gravity constant g (ms^{-2}) and the earth radius r (m) are adjusted for latitude (e.g. Hofmann-Wellenhof & Moritz, 2006).

However, the spatial resolution of the reanalysis product is too coarse (0.25°–30km) and does not account for the possible variation in elevation (and pressure) within each cell of the grid. To avoid this issue, we compute the minimum z_{min} and maximum z_{max} ground elevation found in each grid cell, using the SRTM-90m, a fine-resolution digital elevation model (3 arcsecond–90m; Jarvis et al., 2008).

For each stationary period, we then compute the altitude of the bird from geolocator pressure data. To have a more accurate estimation of

the bird's altitude z_{gl} , we account for the natural variation of pressure using the ERA5 pressure data in the barometric equation,

$$z_{gl} = z_{ERA5} + \frac{T_0}{L_b} \left(\frac{P_{gl}}{P_{ERA5}} \right)^{\frac{R L_b}{gM} - 1}. \quad (2)$$

where P_{gl} is the pressure measured by the geolocator, P_{ERA5} is the surface pressure from the reanalysis data, L_b is the standard temperature lapse rate ($-0.0065 K/m$), R is the universal gas constant ($8.31432 N \cdot m / mol \cdot K$), g is gravity constant, M is the molar mass of Earth's air ($0.0289644 kg/mol$) and T_0 is the standard temperature ($273.15 + 15 K$). As the surface pressure P_{ERA5} changes over space, z_{gl} is computed on each grid cell and thus corresponds to the hypothetical altitude of the bird assuming the bird was in that particular cell.

Finally, we mask out all grid cells where the geolocator altitude z_{gl} is either lower than the minimum altitude z_{min} or higher than the maximum altitude z_{max} for at least 10% of the stationary period. To account for some errors and variability of the time series (e.g. due to temporal offset in the tidal effect), we accept elevation errors within a margin of $\pm 20m$.

This first information extracted from pressure data produces a mask of possible grid cells where the bird could have been, based on the absolute values of pressure and altitude.

2.3.2 | Matching pressure values temporally

The second piece of information extracted from the pressure data quantifies how well the temporal variation of the geolocator's pressure measurements matches the temporal variation of the reanalysis data.

For each stationary period, we quantify the difference between the pressure time series of the geolocator P_{gl} and the reanalysis pressure P_{ERA5} in each grid cell. However, as the influence of altitude is already verified in the previous subsection, we remove the mean error of each stationary period,

$$\epsilon = P_{gl} - P_{ERA5} - (\overline{P_{gl}} - \overline{P_{ERA5}}). \quad (3)$$

We then assess the match of the time series by assuming a normal distribution of the error,

$$f \propto \exp \left(-w(n) \sum_{i=1}^n \frac{\epsilon_i^2}{\sigma^2} \right). \quad (4)$$

where σ is the standard deviation of the error, calibrated at the equipment and retrieval site (value typically ranging between 0.34 and 3.4; see Page 2 in Supporting Information S1). This value mainly accounts for the altitudinal movement of a bird during a stationary period. Because some species live in mountainous areas only during their breeding period (e.g. Eurasian Hoopoe), we used a lower standard deviation during the rest of its journey than the one calibrated at the equipment site.

$w(n)$ accounts for the correlation in the n datapoints of the pressure error time series ϵ and is equivalent to the log-linear pooling weight in

the theory of aggregation likelihood (e.g. Allard et al., 2012; Nussbaumer et al., 2020). As such, $w = 1$ assumes independence of the errors (i.e. the conjunction of probabilities) and $w = 1/n$ essentially averages the error (disjunction of probabilities). We empirically define $w(n)$ as

$$w(n) = \frac{\log(n)}{n}. \quad (5)$$

We outline the rationale for using log-linear pooling and assess $w(n)$ at the calibration periods in the GeoPressure Manual at <https://raphaelnussbaumer.com/GeoPressureManual/likelihood-aggregation>.

For mountain species, where extensive altitudinal change was found, we choose the most frequently occurring altitude level and manually discard the pressure at other altitudes (e.g. 200E and 200A in Supporting Information S2). This can also happen due to differences between roosting and foraging locations (e.g. typical for communally roosting species). If the bird constantly changes altitude, we discard the pressure for that entire stationary period (e.g. 200A). In both cases, we still use the pressure threshold mask without discarding any data. Because this method requires the pressure time series measured from a single elevation, we manually discard pressure datapoints when the bird is at a different elevation. This labelling procedure is outlined in more detail and illustrated with examples in the GeoPressure Manual at <https://raphaelnussbaumer.com/GeoPressureManual/labelling-tracks>. The resulting labelled pressure time series for all tracks can be visualized at <https://raphaelnussbaumer.com/GeoPressureMAT/html/AllTracksPressureWithReanalysis> and in Supporting Information S2.

Finally, we combine the mask of possible locations created in Section 2.3.1 with the likelihood map based on the mismatch of pressure time series generated in Section 2.3.2 to produce a likelihood map of possible bird locations for each stationary period.

2.4 | Creation of position maps from light data

We estimated the likelihood map of the bird's position for each stationary period based on light measurements following the threshold method (Hill, 1994; Hill & Braun, 2001; Lisovski et al., 2020; Lisovski & Hahn, 2012; Montenbruck & Pflieger, 2000).

First, the twilight time is defined automatically as the first and last light of each recorded day, that is, a threshold of 0. We performed a manual editing to remove outliers with TRAINSET (Kapoor et al., 2021).

Then we calibrate the twilight based on the stationary period(s) when the bird was located at the equipment and retrieval site. The calibration is performed directly on the zenith angle of the sun which corresponds to the angle of the sun at the known location of the bird, and at the time of twilight estimated on the geolocator data. We fit the distribution of zenith angle of all twilights of the calibration period with a kernel smoothing function (e.g. Bowman & Azzalini, 1997), allowing to account for any probability distribution of zenith angle (Page 4 in Supporting Information S1). Based on the distribution of the zenith angle, we compute the likelihood

map of the bird for each twilight with the solar equation (Lisovski & Hahn, 2012; Meeus, 1991).

Finally, the likelihood maps of all twilights belonging to the same stationary period are aggregated into a single likelihood map. Because consecutive twilight estimates cannot be assumed to be independent due to the constant or correlated shading effects (e.g. topography, weather, vegetation), we use a log-linear pooling aggregator to combine the likelihood maps. Log-linear pooling relaxes the assumption of independence in the Bayesian aggregation (e.g. Allard et al., 2012; Nussbaumer et al., 2020; Sumner et al., 2009) by combining conditional probabilities as a weighted sum in log space. A constant weight of 0.1 was empirically chosen.

3 | RESULTS

3.1 | Illustration of the method

We apply our method to all the geolocator tracks and compute the likelihood maps for each stationary period. These maps are available in Supporting Information S3 for the Great Reed Warbler (18IC) and on Nussbaumer, Gravey, Briedis, and Liechti (2022) for all other tracks.

In this section, we focus on the first stationary period of the Great Reed Warbler (18IC) and outline the different components of the method with Figure 2.

The typical pressure time series of migrant birds includes a few extended stationary periods (breeding and wintering sites) visible in Figure 2a, as well as multiple shorter stationary periods (migratory stopover sites) visible in Figure 2c. Migratory flight can be recognized by a sharp pressure drop corresponding to high flight altitude (Figure 2a,c), making it possible to identify stationary periods based only on pressure data (i.e. without the use of accelerometer data).

Following the method outlined in Section 2.3, we compute the pressure mask (dark transparency in Figure 2e) and likelihood mismatch map (colour gradient in Figure 2e) for the first stationary period. According to the pressure mask, the range of pressure values measured by the geolocator is compatible with multiple grid cells scattered throughout Europe, roughly corresponding to cells comprising an elevation of 200m. On the contrary, the pressure mismatch map strongly constrains the location to a small number of grid cells.

Since the stationary period selected here corresponds to the known equipment site, we can validate the accuracy of the approach. Indeed, since we did not use knowledge of this equipment site in the method, we can reliably assess the likelihood map. In this specific example, the result is remarkably accurate as the equipment site is found in the most likely cell of the likelihood map. The likelihood map provides a precise estimate with the 90% uncertainty range included in only four cells. The corresponding maps for all tracks can be found in Supporting Information S4.

Figure 2b illustrates the amplitude of natural variations in pressure over time and altitude at the equipment site. We adjust the ERA5 pressure time series at the exact altitude of the equipment

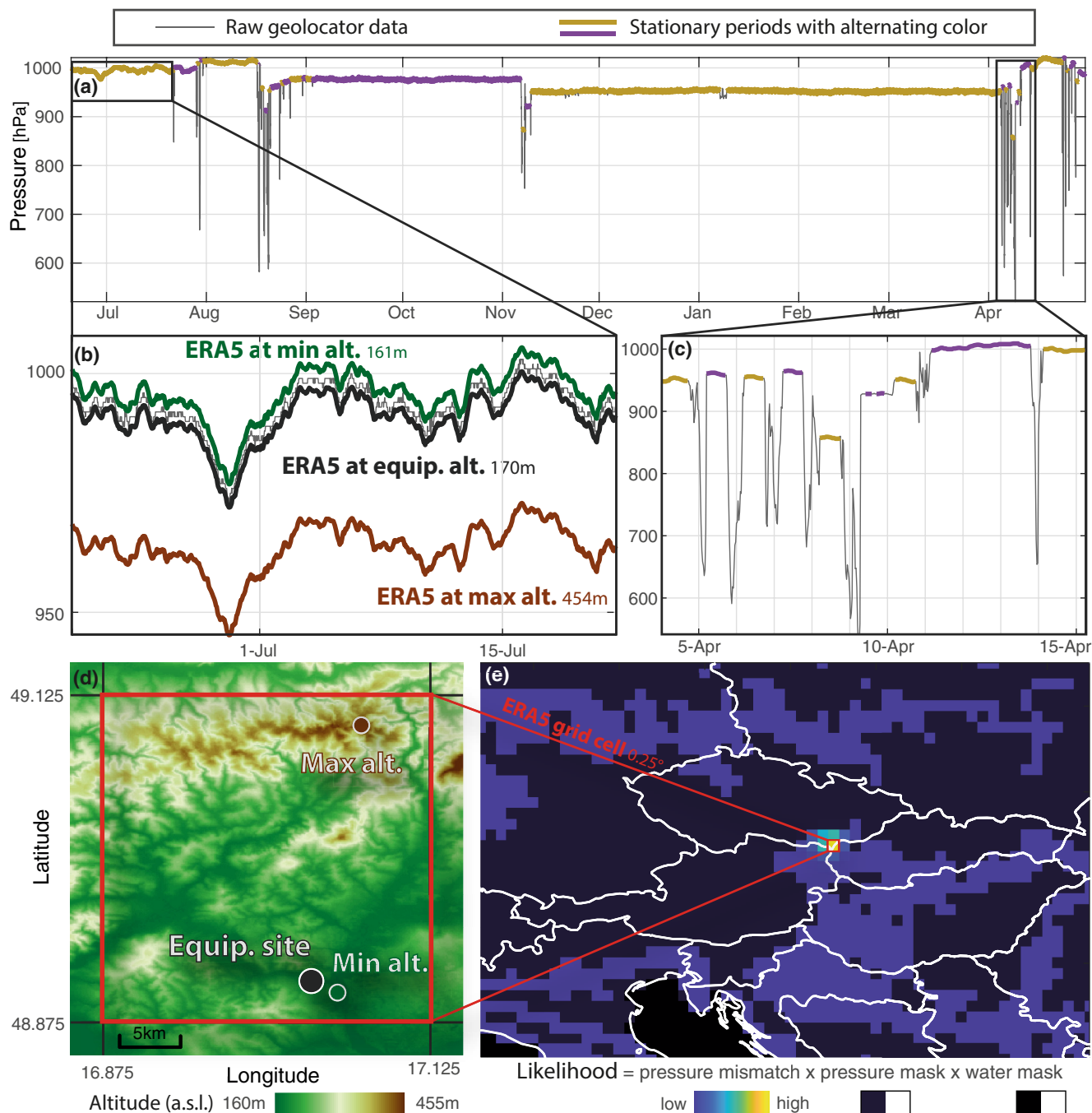


FIGURE 2 Illustration of the method for the first stationary period (equipment site) of the Great Reed Warbler (18IC): (a) Year-round time series of the raw pressure measured by the geolocator together with the cleaned (i.e. outlier removal and smoothed) time series split in consecutive stationary periods (illustrated by alternating colours), (b) Zoom-in on the first calibration period where the location of the geolocator is known (equipment site), (c) Zoom-in on a migration period to illustrate the difference of pressure measurement between flights and stationary periods, as well as among stationary periods, (d) High-resolution (3 arcsecond) digital elevation model on the ERA coarse grid cell (0.25°) covering the equipment site (large black circle), showing the location of the min and max altitudes (green and red circles, respectively), (e) Resulting likelihood map of the first calibration period.

site and display the time series for the minimum and maximum elevations found in this grid cell (Figure 2b,d). We find an excellent match between the geolocator data and the ERA5 time series for the temporal variation (standard deviation of the error of 0.6 hPa) and a small offset for the absolute values (mean of 2.1 hPa).

3.2 | Comparison of pressure and light at equipment and retrieval sites

For each geolocator, we assess the accuracy of light and pressure likelihood maps for the stationary period at the known equipment

site (Supporting Information S4). The likelihood maps of pressure and light are generally consistent. The most likely location on the pressure data-derived map is consistently closer to the known equipment or retrieval site than the most likely location on the light-derived map (42 km vs. 118 km on average), with a single exception (Figure 3). This is the case despite light data being calibrated at these sites.

3.3 | Comparison of pressure and light at the wintering site

In addition to the stationary periods at the equipment site, we compare the likelihood maps of pressure and light for the longest stationary period outside of equipment and retrieval (i.e. corresponding to the nonbreeding site, except for Afrotropical migrants, for which it corresponds to breeding site; Figure 4). Both likelihood maps generally overlap with respect to the general area of the wintering site. However, the distances between the most likely locations differ on average by 303 km (ranging from 108 to 727 km).

3.4 | Comparison of tracks for pressure and light

We qualitatively compare the difference between the light and pressure locations produced for the consecutive stationary periods of the Great Reed Warbler post-breeding migration (18IC) and discuss the complementarity of both sets of information (Figure 5 for 18IC and Nussbaumer, Gravey, Briedis, & Liechti, 2022 for the other tracks).

The likelihood map derived from light data provides a well-defined location of the bird globally, but with high uncertainty at the regional scale. This uncertainty has a strong anisotropy, particularly during the equinox, so that the longitudinal component is more informative than latitude. Moreover, light might be prone to biases, particularly for stationary periods far from the calibration site, where different weather, topography and habitat conditions can be found.

The pressure mask provides information independently of the stopover duration, but the value of this information varies with

altitude: a low pressure corresponding to high altitude refines the possible map to only a few grid cells (e.g. Ring Ouzel), whereas a pressure corresponding to low altitude can be found anywhere (e.g. Sahara).

In contrast, the pressure mismatch map becomes more precise as the length of the pressure time series increases. Yet, it already provides information about the location of the bird with a time series of several hours to a few days. This duration depends on the type of weather system that influences the variation of pressure.

Combining the mask and mismatch, the pressure map provides precise locations (<100 km) for relatively long stationary periods (>5 days) (e.g. 31 July–17 August in Figure 5). Although the precision for shorter stopovers can vary, the pressure map is always well defined locally. Therefore, it can offer a number of different possibilities far from each other (e.g. 29–30 July in Figure 5). In such cases, light information is instrumental to eliminate some of these possible locations. Indeed, a single twilight can be enough to estimate the longitude and refine the locations offered by the pressure data (e.g. excluding the area in Belgium/Germany on the 17–18 September in Figure 5).

Together, these two independent sets of information can help assess the precision and accuracy of each other by assessing their agreement and difference. It then becomes straightforward to visually draw the trajectory of birds with relative confidence. More advanced modelling is required to incorporate a movement model (e.g. Sumner et al., 2009; Wotherspoon et al., 2013) and estimate trajectories between poorly defined areas (e.g. whether the crossing of the Mediterranean Sea occurred on the 17th or 18th of August in Figure 5).

4 | DISCUSSION

4.1 | Advantages of pressure over light geopositioning

Unlike light-level geolocation, the pressure-based approach does not require calibration, making it possible to use the known equipment and retrieval locations for validation. Using those known positions,

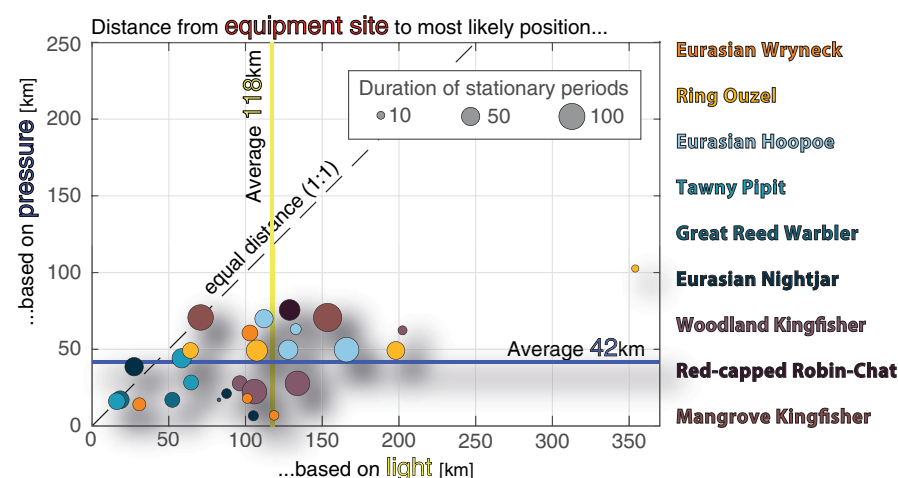


FIGURE 3 Distance from the known equipment (and retrieval) sites to the most likely location according to the likelihood map of light and pressure for all 16 tracks at both the first and last stationary periods (post-equipment and pre-retrieval). Note that an ERA5 grid cell is ~30 km × 30 km. The likelihood maps of light and pressure for those stationary periods are available in Supporting Information S4.

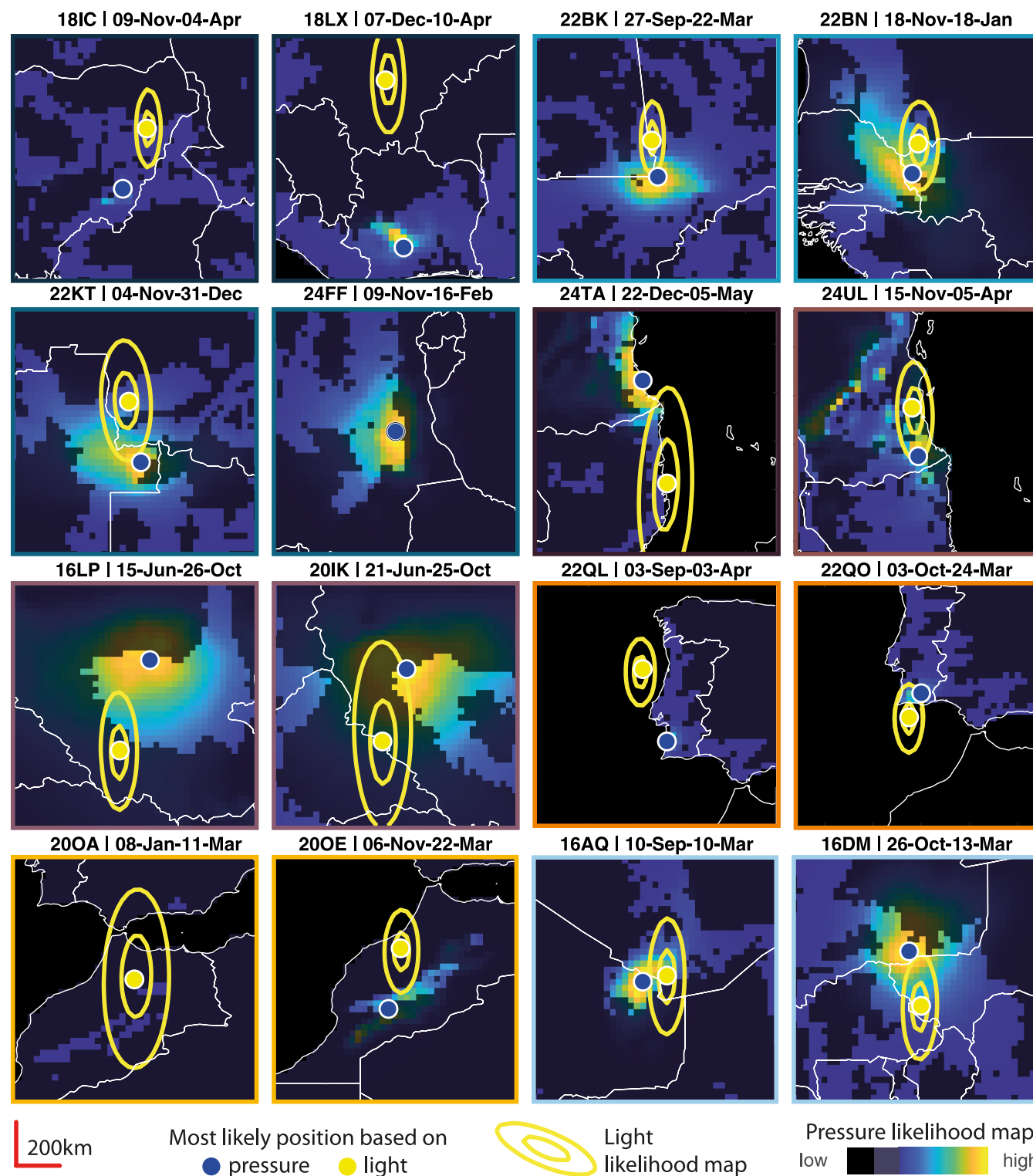


FIGURE 4 Likelihood maps produced by pressure and light data at the sites with the longest duration (generally the wintering site except for the Afrotropical migrants, for which it is the breeding site). The most likely location is symbolized by a blue circle for pressure and a yellow circle for light. The location for the wintering site of Eurasian Nightjar (24FF) could not be determined with light data. Because the quality of the pressure time series was not sufficient for the wintering period of the Ring Ouzel (20OA), only the pressure mask is retained.

we demonstrate that our method is almost three times more precise than light-level geopositioning. This is true even though light data was calibrated at these positions.

Pressure-based geopositioning also extends the reach of species that can be accurately tracked. First, with the higher accuracy

obtained, birds migrating shorter distances, in particular along a north-south axis (e.g. Mangrove Kingfisher, migrating 400 km), can now be accurately tracked. Secondly, in dense foliage situations, light-level geolocators, and, to a lesser degree, archival GPS and telemetry suffer from data transmission issues or erroneous

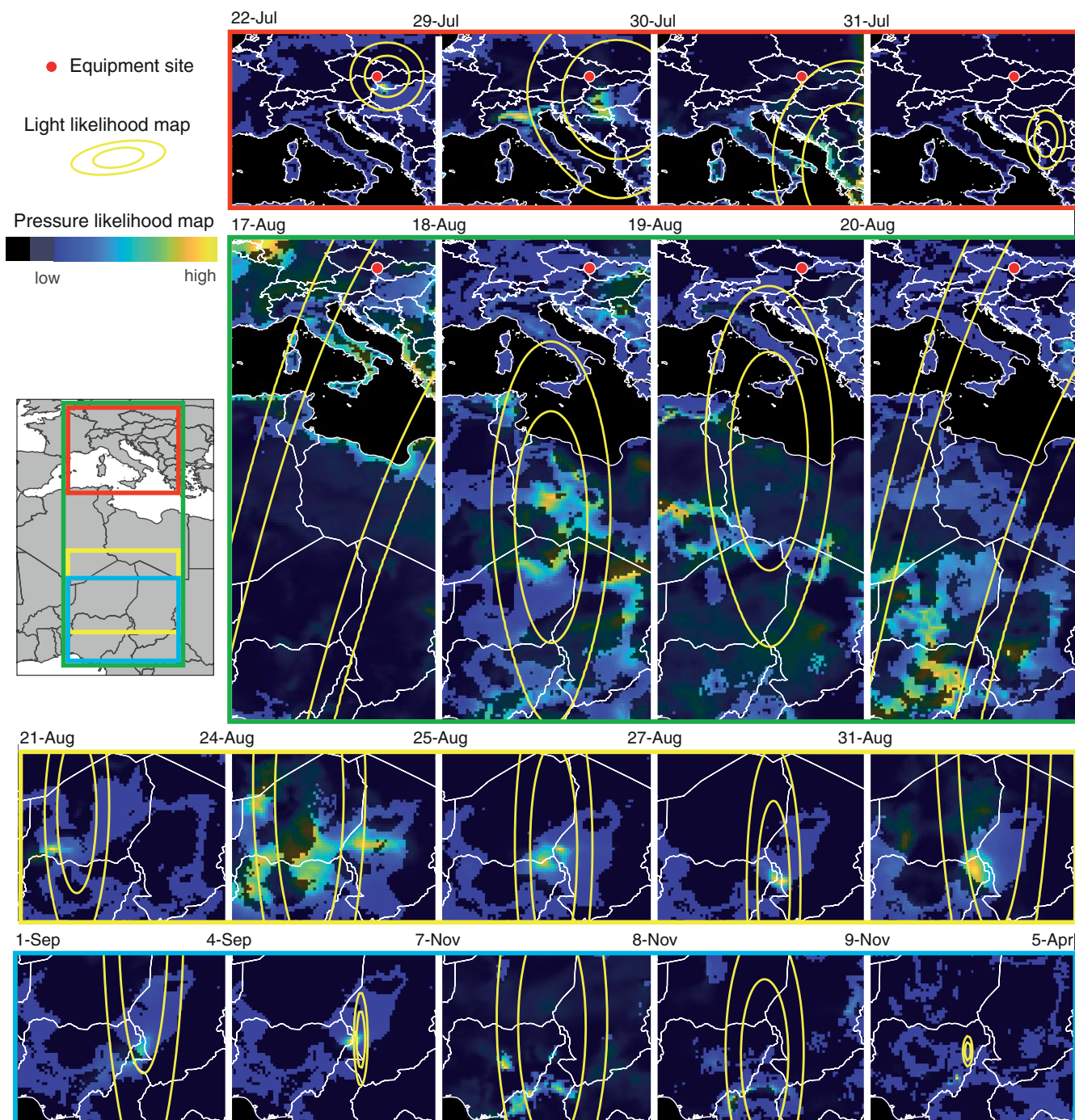


FIGURE 5 Example of the likelihood maps generated for stationary periods greater than 12h during the post-breeding journey of the Great Reed Warbler (18IC), comparing the information from pressure and light. See [Supporting Information S3](#) for similar enlarged figures for 18IC and Nussbaumer, Gravey, Briedis, and Liechti (2022) for all tracks and all stationary periods (incl. <12hr).

measurements, respectively. In contrast, pressure-based geolocation is not sensitive to tree coverage, making it possible to accurately track many forest-dwelling migrant species. Finally, this method can be applied to small nocturnal migratory animals such as bats, owls or small mammals.

Moreover, contrary to the traditional light-based approach, pressure data can provide location information even for short periods on the ground (less than a day). Most importantly, pressure and light positioning are independent and can bring complementary information

(e.g. 17–18 September in [Figure 5](#)). Therefore, combining their likelihood maps further improves geopositioning.

4.2 | Refining birds' altitude with pressure

Once we know the position of the bird, we can account for the temporal variation of pressure (and temperature) in the barometric equation, which allows us to calculate the altitude of a bird with

higher precision (Figure 6 and Supporting Information S5). Indeed, atmospheric pressure varies over time with a standard deviation ranging from 2 to 5 hPa (data from all tracks computed at the calibration site), corresponding to an altitudinal standard deviation of 20–50 m. This opens the door for more precise studies of bird altitudinal movements, which could be particularly relevant for mountain species with altitudinal migration (e.g. Barras et al., 2021).

In addition, based on this high-resolution estimation of altitude, we can further increase the precision of the pressure mask, which currently filters altitude on a 0.25° grid cell. As an example, Figure 7 shows the breeding area of the Mangrove Kingfisher (24UL) with an altitude mask based on the SRTM-30m digital elevation model. This operation enables us to narrow the location of its breeding site to only 200 km². An interactive map of all tracks and stationary periods can be found at <https://rafnuss.users.earthengine.app/view/pressuregeolocator>.

4.3 | Method requirements and limitations

The precision of geopositioning by pressure relies on the small uncertainty of the reanalysis data and pressure sensor relative to the natural spatio-temporal variation of pressure. Therefore, we can only reliably track movements over tens of kilometres using ERA-5 data (~10 km for ERA5-Land; Muñoz Sabater, 2019). A critical factor limiting this precision is the altitudinal movements of the bird, which, by influencing the pressure measured by the geolocator, alter the match between the pressure time series and the reanalysis data. Consequently, this method is not suitable for airborne birds (e.g. swifts), which do not spend repeated and extensive periods of time at the same elevation, nor for marine wildlife because of the large changes in pressure with water depth.

In this study, we show that we can apply our approach to mountainous species (e.g. Ring Ouzel), despite their irregular altitudinal movements, by identifying periods where the bird remains at the same elevation during a given stationary period. Even in the rare case where the Ring Ouzel constantly changed its elevation, the pressure mask on its own (i.e. without pressure mismatch map) was sufficient to restrict possible locations, since such ranges of altitude were only found in the few cells containing high altitudes (e.g. 200A in Figure 4).

For optimal results, we suggest collecting pressure data with a temporal resolution of at least 1 h to match the ERA-5 resolution (ideally ≤30 min). Identification of stationary periods requires a higher resolution (~minutes) of acceleration and/or pressure data. We refer readers to Dhanjal-Adams et al., (2022) for further information on identifying stationary periods with other types of data and methods.

4.4 | Importance of accurate labelling

Well-defined stationary periods with smooth pressure time series are critical to accurately estimate the bird's position. This generally requires meticulous manual editing of the time series, which is time-consuming and complex. Indeed, the identification of migratory activity can be challenging for species moving at low pace with multiple stops and potentially feeding at the same time (e.g. Tawny Pipit or Eurasian Nightjar). Furthermore, altitudinal changes within a stationary period (e.g. daily commute or adjustment flight at stopover arrival in the morning) can be hard to detect, potentially leading to incorrect position estimates. Accelerometer data can be particularly useful in this context to identify stationary periods. A dedicated user guide was created to facilitate this labelling task, including tips and test codes to check the quality of the

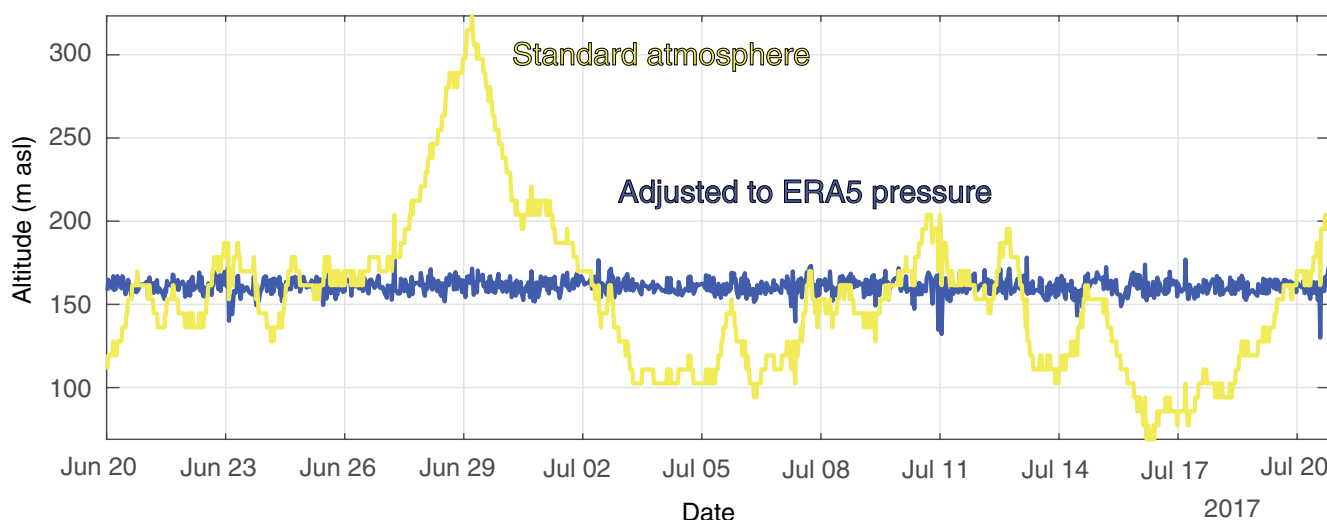


FIGURE 6 Altitude of the Great Reed Warbler at its equipment site. The altitude is computed from the pressure measurement of the geolocator using the barometric equation with (1) the standard atmosphere values ($T_0 = 288.15$ K and $P_0 = 1013.25$ Pa) and (2) the ground-level pressure, temperature and elevation of ERA5. The standard atmosphere artificially generates altitudinal movement of the bird caused by the natural variation of pressure. The full elevation profiles for all tracks are available in Supporting Information S5.

4.7 | Trajectory modelling

More accurate estimation of a bird's migratory trajectory can be achieved by combining all available information (e.g. light data, pressure data, sea surface temperature) in a movement model that accounts for realistic movements of the animal. This is typically achieved with a state-based model/hidden Markov model (e.g. Jonsen et al., 2013; Nielsen & Sibert, 2007; Rakhimberdiev et al., 2015). The likelihood maps produced in this work can be incorporated into any of these models, similarly to the light-derived maps in Basson et al. (2016).

Taking advantage of the well-defined pressure likelihood maps, we introduce in a separate paper (Nussbaumer, Gravey, Briedis, Liechti, & Daniel, 2022) a new modelling framework which can solve the movement model exactly (i.e. no MCMC) while integrating information of pressure, light, flight duration as well as wind support (e.g. Werfeli et al., 2022).

5 | CONCLUSIONS

Our findings provide a good argument for pressure-based geolocation to become the standard method for affordable lightweight tracking devices. The presented method can work with pressure measurements alone, thus making it possible to use with extremely light tracking devices (e.g. 0.37g; Shipley et al., 2018), which rely on simple, common and affordable technology with a low expected failure rate. The key requirements of this method are that (1) animals migrate several hundred kilometres at least, (2) animals spend prolonged time (several days) at an identical site (± 10 km horizontally; ± 10 m vertically) ideally over multiple days and (3) these periods are identifiable from the geolocator measurements (e.g. pressure and/or accelerometer). This new method broadens the application of lightweight tracking devices to a range of new species: short-distance migrants, forest dwellers, nocturnal animals, small mammals and altitudinal migrants.

AUTHOR CONTRIBUTIONS

Raphaël Nussbaumer and Mathieu Gravey conceived the ideas and designed the method; Felix Liechti collected the data; Raphaël Nussbaumer performed the numerical implementation and analysis; Raphaël Nussbaumer created the figures and wrote the original draft; Felix Liechti and Martins Briedis reviewed and edited the manuscript. All authors critically contributed to the drafts and gave their final approval for publication.

ACKNOWLEDGEMENTS

This research was funded by the Swiss National Science Foundation (grant no. 191138). The Swiss Federal Office for Environment contributed financial support for the development of the geolocators (UTF-Nr. 254, 332, 363, 400). We are grateful to our colleagues from our institute Steffen Hahn, Martins Briedis, Silke Bauer, Michael Schaub and to our external collaborators Arnaud Barras, Ruben Evans, Samuel Temidayo Osinubi, Petr Prochazka and Dirk Tolkmitt sharing their data with us. Data from Hersbach et al. (2018) was downloaded from the

Copernicus Climate Change Service (C3S) Climate Data Store (<https://cds.climate.copernicus.eu>). The results contain modified Copernicus Climate Change Service information for 2020. Neither the European Commission nor the ECMWF are responsible for any use that may be made of the Copernicus information or data it contains.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.14043>.

DATA AVAILABILITY STATEMENT

The datasets supporting the conclusions of this article are available at the following locations:

- GeoPressureMAT (<https://github.com/Rafnuss/GeoPressureMAT>) contains the MATLAB code used to perform the analysis and label the light and pressure tracks. An interactive visualization of the labelled time series can be found at <https://raphaelnussbaumer.com/GeoPressureMAT/html/AllTracksPressureWithReanalysis.html>
- GeoPressureAPI (<https://github.com/Rafnuss/GeoPressureAPI>) contains the code and documentation for the JSON API that computes the mismatch between pressure time series and ERA-5 in Google Earth Engine.
- The GeoPressureR package (<https://raphaelnussbaumer.com/GeoPressureR>) provides the basic functions to perform the same analysis for other tracks.
- The GeoPressureManual (<https://raphaelnussbaumer.com/GeoPressureManual>) aims to guide new users of GeoPressureR through the successive steps to follow.
- GeoPressureTemplate (<https://github.com/Rafnuss/GeoPressureTemplate>) is a Github repository template that provides the project code folder structure to kick-start a project.
- The Google Earth app (<https://rafnuss.users.earthengine.app/view/pressuregeolocator>) illustrates the resulting likelihood map of positions for each track and stationary period, as well as the corresponding NVDI map and habitat classification.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1 Histograms and variograms of light and pressure.

Supporting Information S2 Pressure timeseries.

Supporting Information S3 Likelihood maps for the Great Reed Warbler (181C).

Supporting Information S4 Comparison maps of light and pressure.

Supporting Information S5 Bird altitude over time.

How to cite this article: Nussbaumer, R., Gravey, M., Briedis, M., & Liechti, F. (2023). Global positioning with animal-borne pressure sensors. *Methods in Ecology and Evolution*, 14, 1104–1117. <https://doi.org/10.1111/2041-210X.14043>