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METHODOLOGY

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Using GPS and accelerometer data to remotely detect breeding events in two elusive ground-nesting steppe birds

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Abstract

Background Modern biologging technologies allow researchers to gain a better understanding of animal movements, offering opportunities to measure survival and remotely study the breeding success of wild birds, i.e., by locating nests. This is particularly useful for species whose nests are difficult to find or access, or when disturbances can impact the breeding outcome. We developed and validated, with field data, a framework to detect nesting events by two sandgrouse species, the black-bellied (*Pterocles orientalis*) and pin-tailed sandgrouse (*Pterocles alchata*), using GPS and Overall Dynamic Body Acceleration (ODBA) data. Sandgrouses are ground-nesting, cryptic, and elusive birds with biparental incubation efforts. Because both sexes take turns to incubate, a novel framework considering when tagged individuals are on incubation duty or not needs to be designed to detect nests.

Results We tagged 52 birds with high-resolution GPS devices to monitor their breeding during 2021–24. Using remote tracking and field data from the first 2 years (2021–22), we first determined sex-specific time windows for incubation to maximise differentiation between incubation and non-incubation behaviours. We then used a threshold-based classification to identify incubation days and inferred the minimum number of successive incubation days needed to correctly identify a nesting event. We show how ODBA and GPS data can be used to successfully detect nests incubated for only 2 or 3 days. GPS-only data or combined GPS-ODBA data had a success rate of around 95%, whereas ODBA-only data had a success rate of 100%. Cross-validation using data from 2023 to 2024 confirmed the model's performance, showing an overall success > 90% for GPS-only and ODBA-only data and of 85% for combined GPS–ODBA data.

Conclusions By accurately identifying nesting events, our framework offers new opportunities to study the breeding of conservation-dependent species. Besides its applicability to ground-nesting species with biparental care and sex-specific incubation schedules, the framework can be adapted to other bird species sensitive to disturbances or with inaccessible nesting sites. By doing so, it reduces the need for nest visits and associated disturbances, as well as the carbon footprint and expenses associated with fieldwork.

Keywords Biologging, Breeding ecology, Nest detection, ODBA, Sandgrouse, *Pterocles alchata*, *Pterocles orientalis*, Steppe bird conservation, Tracking data

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[†] João P. Silva and François Mougeot have equal supervision and contribution to the final manuscript.

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Background

Farmland birds, and steppe-birds in particular, are declining at alarming rates worldwide [1–3]. The Iberian Peninsula represents an important European stronghold for numerous steppe birds [4–6], where farming intensification has led to significant population declines (e.g., [6, 7]), and the recent expansion of renewable energy production infrastructures poses new threats [8–10]. In addition, many farmland birds are ground-nesting and vulnerable to a wide range of predators, which can severely impact their breeding success [11–13]. Low productivity can negatively impact population growth, particularly in ground-nesting species (e.g., [14, 15]). Therefore, studying breeding performance and identifying the main causes of breeding failure are key to understand the drivers of declines and population viability [16–20]. However, research on the reproductive biology of steppe birds has been hindered by the difficulty of detecting and monitoring nests due to their ground-nesting habits, cryptic plumage, elusive behaviour, and sensitivity to human disturbances [21–24]. Challenges associated with monitoring the breeding of these species can make fieldwork time consuming, expensive, and inefficient. Moreover, the presence of researchers in nesting areas may cause disturbances that could inadvertently contribute to reproductive failure (e.g., [25]).

Modern biologging technologies enable researchers to remotely gather high-resolution spatiotemporal and sensor data (e.g., acceleration, light intensity or temperature) and investigate crucial aspects of a species' life history and behaviour, including reproduction (e.g., [17, 20, 26–28]). By applying these new technologies, researchers can get a better understanding of the species' reproductive biology, such as incubation rhythms (e.g., [17, 28]), energy expenditure (e.g., [29]) or nest survival, and can determine breeding success and the key factors influencing it (e.g., [16, 20, 26]), without the need of visiting nests and disturbing breeding birds. GPS tracking data were shown to be effective in the identification of breeding attempts in several species (e.g., [26, 30, 31]). However, movement data alone can occasionally overlook nesting attempts that fail early during incubation or inaccurately classify their duration or fate (e.g., [30, 31]). Integrating GPS with acceleration (ACC) data can improve the efficiency and accuracy of nest detection, providing in-depth understanding of individual daily behaviours [20, 32]. By employing this integrated method, researchers can differentiate breeding behaviours from others with similar movement patterns, such as roosting or foraging, and distinguish between low breeding propensity and high failure rates [20, 32]. Although this approach has many benefits, researchers have just recently started to combine GPS and ACC data to study avian breeding performance. A first threshold-based method, presented by Schreven et al. [20], relied on average daily overall dynamic body acceleration (ODBA) estimates, derived from 3D ACC data, and the daily time spent within a consistent radius area for more than three consecutive days, to detect and characterize nesting attempts by female pink-footed geese (*Anser brachyrhynchus*). Nests sites were located by calculating the median coordinates on days when time and ODBA values dropped below pre-determined thresholds. In another recent study, Ozsanlav-Harris et al. [32] developed a threshold-based scoring system, using daily ODBA estimates, daily median net displacement values, and the distance between successive median daily locations over a 3-day window, to successfully identify nesting attempts by female Greenland white-fronted geese (*Anser ablifrons flavirostris*).

In the current study we tested the potential of GPS and ODBA data, isolated or in combination, to detect nesting attempts by two ground-nesting steppe birds, the black-bellied sandgrouse (*Pterocles orientalis*, Linnaeus 1758) and pin-tailed sandgrouse (*Pterocles alchata*, Linnaeus 1766). Like other Iberian steppe birds, both species are declining and face an unfavourable conservation status [33–35]. To date, there is limited understanding of their reproductive biology, especially in natural populations, due to difficulties in finding and monitoring nests without observer interference [17, 23, 36, 37]. Sandgrouse chicks are nidifugous, i.e., chicks leave the nest soon after hatching [23, 37], so nests must be detected during incubation. Biparental efforts and alternating incubation schedules (the male incubates at night and the female during the day; [17, 19, 36]) further limit the applicability of existing methodologies for remote sandgrouse nest detection, since they were primarily developed and tested for species with uniparental incubation efforts and prolonged daily nest attendance [20, 32].

Given the negative trends of both species, their sensitivity to disturbances and ground-nesting strategy, which makes them vulnerable to predation or nest destruction during agricultural practices, there is a need to develop and validate monitoring tools that minimize the potential negative impacts of field work during breeding while providing valuable information for conservation. Here we used state-of-the-art biologging technology to develop and validate a framework that allows to remotely identify sandgrouse nesting attempts. By exploring the performance and complementarity of GPS and ODBA data for nest detection, our aim was to demonstrate the effectiveness of biologging for remotely detecting breeding attempts by ground-nesting farmland birds, and particularly by species with biparental incubation efforts. We discuss the limitations and advantages of the approach, and how it can be optimized and adapted to other species.

Methods

Study area and species

This study was conducted in three semi-arid areas of southwestern Iberia: the Castro Verde (37°41′46.5″N 7°54′47.0″W) Special Protection Area (SPA) and Vale do Guadiana (37°37′54.7″N 7°35′42.2″W) Natural Park in Portugal, and the SPA of La Serena y Sierras Periféricas (38°48′35.1″N 5°20′17.5″W) in Spain. These flat, almost treeless regions within the Mediterranean biome are mainly dominated by traditional cereal farming and extensive pastoral habitats with grasses and dwarf shrubs, also designated as pseudo-steppes [24, 38].

Sandgrouses (family *Pteroclidae*) are medium-sized birds found in arid and semi-arid regions of the Old World [39–42]. In Europe, the black-bellied (BBS) and pin-tailed sandgrouse (PTS) find their main population stronghold in the Iberian Peninsula [5, 34, 35]. Sandgrouses are monogamous, nest in open areas with low vegetation cover and lay two to three eggs in a shallow ground depression [17, 36, 43] between April and September [19, 23, 36]. Incubation lasts 24–26 days for BBS and 19–22 days for PTS [23, 36, 43]. Chicks take 3–4 weeks to fledge [37]. Relaying occurs after failure, but pairs only produce one successful clutch per year [19, 36].

Sandgrouse capture and data collection

Between February and May 2021–24, we captured and tagged 29 BBS (10 in Portugal, 19 in Spain) and 23 PTS (exclusively in Spain; see Table S1, Additional File 1). Captures were performed at night following the methodology described in Benítez-López et al. [44]. Solar-powered, self-charged GPS–GSM tags were fitted to sandgrouse using a Ribbon Teflon thoracic harness. In 2021, nine BBS were tagged with 9 g OT-9-3GX tags (Ornitela UAB, Lithuania) and one PTS with a 5 g Druid Mini tag (Druid Technology Co., Ltd.). Between 2022 and 2024, 20 BBS and 22 PTS were tagged with 6 g Druid Mini tags (Druid Technology Co., Ltd.). Tags (including harness) weighted less than 2% of the birds' body weight (mean ± SD of 1.61 ± 0.37% for BBS and 1.84 ± 0.15% for PTS). Ornitela tags collected GPS fixes (six per burst) and raw 3D ACC data at 20 Hz for 4 s every 20 min, with reduced night-time data collection to save battery and improve performance. Druid tags recorded GPS fixes every 30 min and ODBA readings every 10 min at 25 Hz. GPS data from both tags were used for nest detection, but we only used ODBA data from Druid tags (every 10 min), as Ornitela tags' temporal resolution (every 20 min) lacked precision to determine the timing of incubation shifts (see below). Data, in UTC + 0, was transmitted daily through the Global System for Mobile Communications.

Detection of nesting attempts and field validation

Between May and October 2022–24, we detected 123 nests (51 PTS and 72 BBS; Table S1, Additional File 1) using visual assessments of GPS and ODBA data (low mobility and body motion—ODBA values—during incubation). Nest coordinates were estimated using the centroid of the GPS fixes collected during incubation. Most nests (51 PTS and 64 BBS) were visited *in loco* either during incubation (after 15 days), after failure, or post-hatch, to confirm nesting and its outcomes. Additionally, 21 nests (four PTS and 17 BBS) were detected from data collected in 2021 (Table S1, Additional File 1), and one BBS nest was visited in Portugal post-hatch.

Developing a protocol to remotely identify nesting attempts

To mechanistically identify breeding attempts, we initially developed a framework using GPS and ODBA data collected during 2021–22 (Part 1—*i*–*iv*; Fig. 1). We then validated the framework's efficiency in detecting (1) incubation days and (2) nesting attempts, using ground-truth data from fieldwork and a probabilistic methodology (Part 2—*v* and *vi*; Fig. 1). Finally, we cross-validated the results using an independent set of sandgrouse nesting attempts remotely detected and field validated during 2023–24 (Part 2—*vii*; Fig. 1). Different sample sizes (number of nests and tagged individuals) were used for each step (Table S2, Additional File 1). Further details on terminology and the steps (Fig. 1) are also provided in Supplementary Texts 1 and 2, Additional File 1.

Part 1: Nest detection framework

i) Using ODBA data to determine the timing of incubation shifts

To develop the nest detection framework, we initially tested if ODBA records at 10-min intervals could be used to determine when incubation shifts between males and females occurred. Males incubate at night and females during the day, so we expected a marked change (shift) in ODBA values when a bird stops or resumes incubation (see Fig. S1, Additional File 1). ODBA data from three tagged pairs and six nests (Table S2, Additional File 1) were used to simultaneously compare the time of male and female daily shifts.

After converting timestamps to local time, we inspected ODBA data to determine the times of putative morning (*mShift*) and evening (*eShift*) incubation shifts for each individual, day, and nesting attempt. The last day of incubation (hatch or failure) and male's first day of

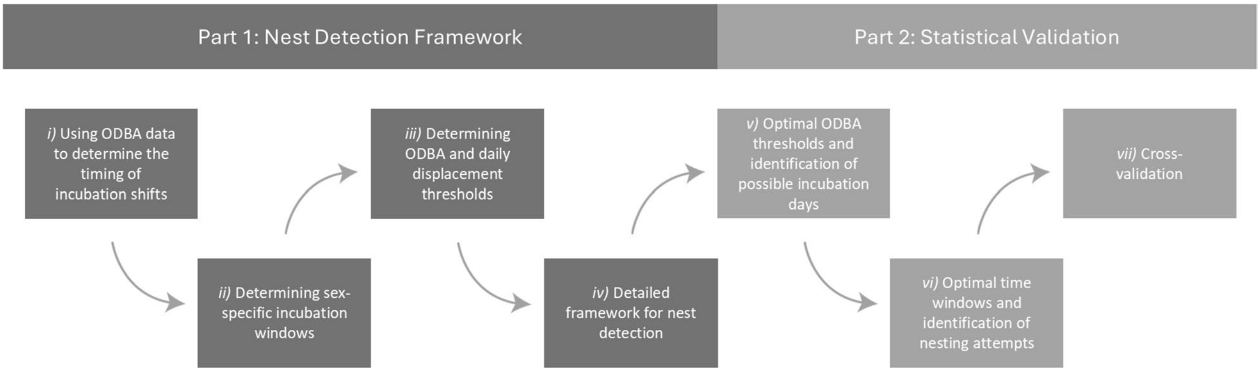

Fig. 1 Overview of the workflow followed to develop the framework to remotely detect breeding events. We initially developed the framework for nest detection (Part 1; steps *i* to *iv*) and then applied a probabilistic approach (Part 2) using ground-truth data collected from field work, to assess the frameworks' capacity to detect nesting attempts (steps *v* and *vi*). Finally, we cross-validated the results obtained in step *vi* to ensure the framework was not overfitted to the training data set (step *vii*). See Supplementary Text 2, Additional File 1 for a detailed overview of the workflow

incubation (no *mShift*) were excluded from the analyses. We determined the time of 93 putative *mShifts* and 102 *eShifts* for females and 104 *mShifts* and 115 *eShifts* for males.

Next, for each pair, nesting attempt, and incubation day, we calculated the time differences between female and male putative shifts (for *mShifts* and *eShifts)* to confirm that shift times were accurately determined using ODBA data. We expected differences between female and male shifts to be close to zero, as birds avoid leaving the nest unattended when switching incubation roles [17]. We also expected male morning shifts to coincide or precede female's shifts (female *mShift* ≥ male *mShift*), and female evening shifts to coincide or precede male's shifts (female *eShift* ≤ male *eShift*). Deviations from zero were expected to be small, positive for morning differences and negative for evening differences.

ii) Determining sex-specific incubation windows

Subsequent analyses of ODBA and GPS data were limited to "incubation windows", representing daily periods when males or females incubate. We aimed to identify the best time-windows that clearly distinguished incubation from non-incubation behaviours, reducing false positives from repeated roosting or feeding sites, or low daytime activity.

To determine the best windows, we initially assessed the consistency of incubation shift times among species, individuals, and days using a repeatability analysis (see [17, 45, 46]). We extracted 1558 shift times (409 *mShifts* and 476 *eShifts* for females and 312 *mShifts* and 361 *eShifts* for males) using ODBA patterns (see step *i*) from 25 incubating birds carrying Druid tags (Table S2, Additional File 1). We calculated an "adjusted repeatability" using the R package *rptR v0.9.22* [17, 47] to assess the consistency of shift times, which were standardized relative to sunrise (*mShift*—sunrise) and sunset times (sunset—*eShift*) to account for variations along the breeding season. Daily sunrise and sunset times were extracted using the *sunriset* function of the R package *suntools v1.0.0* [48]. A generalised linear mixed model (GLMM) including individual breeding events as random factors was used to assess repeatability. We expected shift times to be more consistent within than between clutches [17].

Next, we examined daily ODBA patterns of each sex during different breeding stages (prelaying—1 month before laying, laying, incubation, and chick rearing) to identify the best window limits. We used data from 19 nests that completed the expected incubation period (Table S2, Additional File 1) to account for variances in nest attendance throughout incubation. For each nest and stage, ODBA values were categorised by their timestamp every c.a. 14 min. We then extracted each stage's ODBA pattern by averaging ODBA values of each class. Mid-day was estimated as the time halfway between sunrise and sunset. By comparing these ODBA patterns, we selected the best possible 2-h incubation windows for males relative to sunrise, and for females relative to mid-day, ensuring that all individuals were incubating during these time windows. Finally, we evaluated the window efficiency by comparing average daily window ODBA values ("AvODBA"), and the distance moved between the average window location and that of the previous day (Incubation Window Daily Displacement; IWDD) during different breeding stages.

iii) Determining ODBA and daily displacement thresholds

a. ODBA thresholds

We determined ODBA threshold values using the 19 nests outlined in step *ii* (see Table S2, Additional File 1) to infer the daily reproductive status (incubation or non-incubation) of tagged individuals using ODBA readings collected during the incubation windows. We started by classifying daily ODBA records as incubation "1" and non-incubation "0" and removed values above 2000 that possibly represented activity peaks associated with disturbances. AvODBA values were then estimated during the incubation window by sex (229 incubation and 364 non-incubation days for males; 263 incubation and 307 non-incubation days for females). We then used a GLMM with binomial error distribution and individual identity as a random factor to predict incubation probability from AvODBA values. We tested if the relationships between incubation probability and AvODBA differed between species (BBS vs. PTS) and sexes (Male vs. Female) using the interactions AvODBA*Sex and AvODBA*Species in our initial models and sequentially removing non-significant interactions. Using the best modelled response curve, we determined AvODBA threshold values for incubation probabilities of 0.70, 0.75 and 0.80.

b. GPS position errors and daily displacement values

Different devices may provide different location errors. To determine the precision of Ornitela and Druid tags, we started by filtering GPS data (see Supplementary Text 3, Additional File 1) to remove large location errors that were beyond the species´ step size (0.63% of fixes removed; see [49]) and records linked to large movements or activity peaks. Next, we used window GPS positions of known incubating birds (see Table S2, Additional File 1) and calculated the distance to nest coordinates to obtain positioning errors during incubation. The average location errors (mean ± SD) were of 8.0 ± 24 m for Ornitela tags ($n = 1971$ locations), and 30.84 ± 92.52 m for Druid tags ($n = 1894$ locations). We used these values as IWDD thresholds (8 m for Ornitela and 31 m for Druid tags) to infer potential incubation days based on daily displacement between incubation windows.

iv) Detailed framework for nest detection

Using pre-determined incubation window limits and AvODBA or IWDD thresholds, our conceptual framework (Fig. 2) allowed to distinguish incubation from non-incubation days, and to identify sandgrouse nesting attempts based on a minimum succession of incubation days. This workflow was implemented in R and is available at https://github.com/GFerraz97/RemoteNestDetection.git, along with worked examples. The framework has three main steps:

a) Data preparation

Initially, individual's ODBA readings were georeferenced using average daily GPS coordinates to assign sunrise, sunset, and mid-day times. Then, GPS and ODBA files were updated with information on tagged individuals, such as sex or type of device (see dictionary format at https://github.com/GFerraz97/RemoteNestDetection.git) to define incubation windows and assess possible incubation days. Timestamps were converted to local time; GPS and ODBA data were filtered (see Supplementary Text 3, Additional File 1) to remove outliers and records linked to large movements or activity peaks.

b) Annotation of putative incubation windows

Sunrise, sunset and mid-day times were extracted for each record (see step *ii*) and converted to the data time zone. ODBA and GPS files were then divided based on predefined incubation windows (see step *ii*), keeping for further analyses only records within each day's window, which differed for males and females.

c) Nest detection

AvODBA and IWDD values were determined to identify putative incubation days. First, we calculated daily AvODBA values and average coordinates (during the incubation window) and then calculated a daily displacement, measured as the distance between the average window location and that of the previous day. AvODBA and IWDD values were compared to established thresholds, and days below the thresholds were labelled as possible incubation days. IWDD thresholds were based on GPS error estimates for each tag type (see step *iii*), while AvODBA thresholds were determined during framework validation (see below). When combining ODBA and GPS data, days were labelled as incubation days when both AvODBA and IWDD values were below their respective thresholds. To reduce false positives from behaviours with identical movement or ODBA signatures, nesting attempts were identified when thresholds were met for a minimum number of

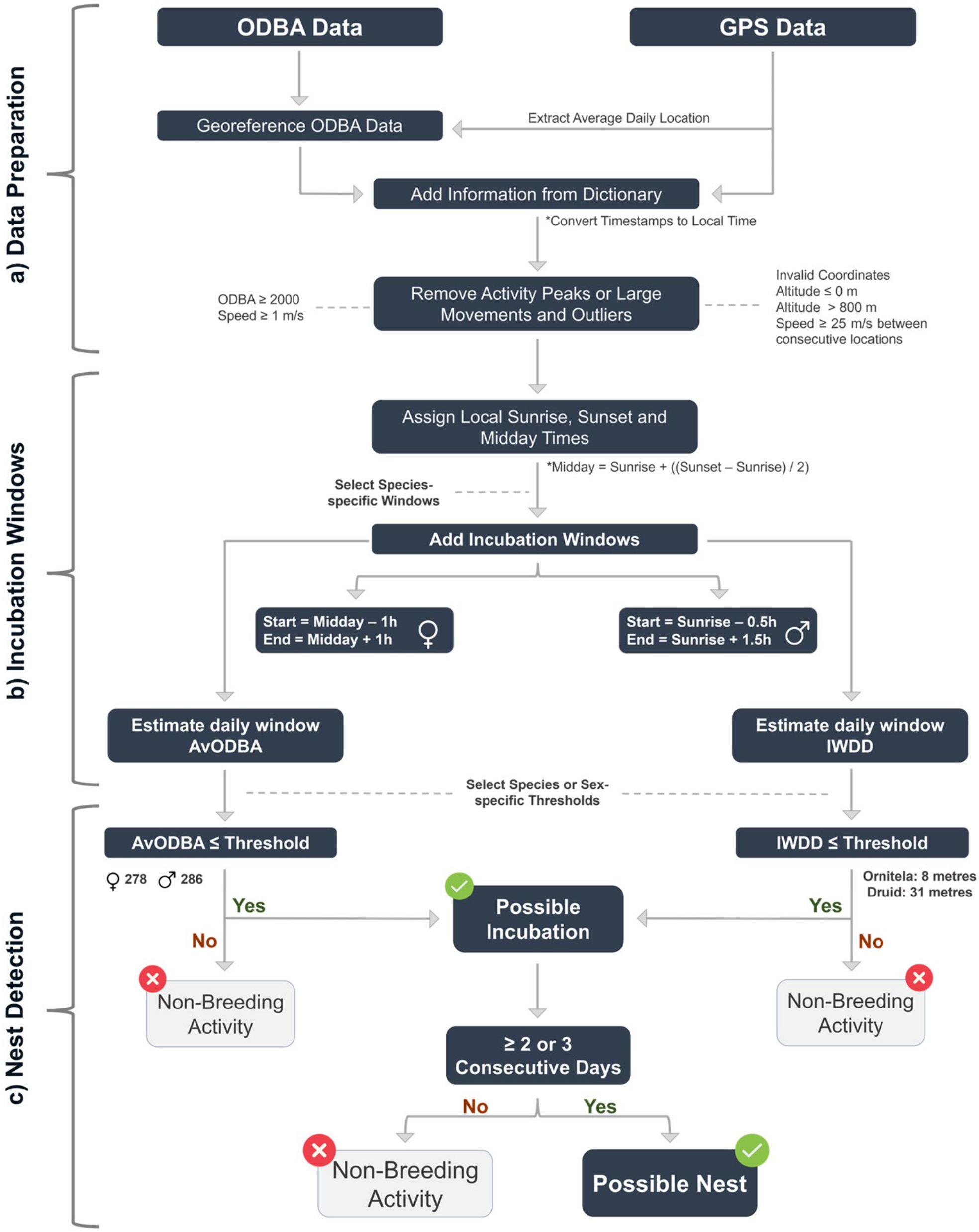

Fig. 2 Conceptual framework to identify nesting attempts using GPS and ODBA data. Window limits for each sex were estimated by comparing average daily ODBA patterns between incubation and non-incubation periods. We calculated threshold values from the AvODBA values on incubation and non-incubation days, as well as the position error of each tag on incubation days. Days with AvODBA and/or IWDD values lower than the thresholds were labelled as possible incubation days. Nesting attempts were identified when AvODBA and/or IWDD values fell below the thresholds for a minimum of 2–3 consecutive days

consecutive days (see below). Finally, nest locations were determined as the median daily window coordinates associated to each detected nesting attempt, which is more robust to the presence of outliers.

Part 2: Statistical validation

The framework's (Fig. 2) capacity to identify nesting attempts using GPS or ODBA data was assessed using a probabilistic methodology frequently employed in machine learning, by calculating precision (*Pr*), recall (*Rc*; or sensitivity) and the proportion of misclassified days or periods (*MsD* or *MsP*). Additionally, we calculated *F-score* values (ranging between 0 and 1), which are commonly used to assess which parameters of a model provide the best balance between precision and recall (see formulas in Supplementary Text 4, Additional File 1; [32, 50, 51]). Better model performance is associated with higher *F-score* values (closest to 1). Overall success rates, i.e., the number of correctly identified nests, were determined using recall values.

v) Optimal ODBA thresholds and identification of possible incubation days

The capacity of the framework to identify incubation days was evaluated using ground-truth data from individuals whose nests were visited during incubation (see Table S2, Additional File 1). Data from 13 individuals carrying Druid tags were used to assess the performance of ODBA-only data (366 incubation and 1182 non-incubation days) or combined GPS–ODBA data (370 incubation and 1195 non-incubation days). AvODBA thresholds were tested for each sex at incubation probabilities of 0.70, 0.75, and 0.80 (see step *iii*). The performance of GPS-only data was tested using 16 individuals (449 incubation and 1505 non-incubation days) carrying Druid or Ornitela tags and device-specific distance thresholds (see step *iii*).

To address uncertainties around the onset of incubation and false positives from the laying period, we conducted performance tests using all incubation and non-incubation days, and then removing 5 days before and after the incubation onset. The last day of incubation was excluded (sandgrouse behave differently during hatching or nest failure), as well as the last day of transmission to avoid inconsistencies due to season end or logger failure. Since both analyses yielded similar results, we present only the validation using the most inclusive data set.

vi) Optimal time windows and identification of nesting attempts

The capacity to detect nesting attempts was evaluated using ground-truth data from nests visited during incubation or with post-incubation evidence (e.g., eggshells, chicks; Table S2, Additional File 1). Data from 20 individuals carrying Druid devices were used to evaluate the potential of ODBA-only data or combined GPS–ODBA data (37 incubation and 64 non-incubation periods). The potential of GPS-only data was evaluated using 25 individuals carrying Druid or Ornitela devices (45 incubation and 81 non-incubation periods).

Nest detection using the proposed framework requires several consecutive days flagged as positive incubation. To determine the minimum needed, we tested the framework's performance using time periods ranging from two to seven consecutive days. The framework's performance was evaluated by comparing correctly or incorrectly identified nesting attempts during incubation and non-incubation periods. Laying days were added to female nesting periods according to clutch size [23, 36]. Two days were added to two-egg clutches and 4 days to three-egg clutches. A 4-day period was added for nests with unknown clutch size.

vii) Cross-validation

To avoid overfitting the framework to the training data set, we cross-validated the results obtained in step *vi* using an independent set of ground-truth nests detected and field-validated in 2023–24 (Tables S1 and S2, Additional File 1). As in the previous step, we only considered nests visited during incubation or with post-incubation evidence (Table S2, Additional File 1): 42 nests for analyses with GPS-only data and 34 nests for analyses with ODBA-only data or combined GPS–ODBA data. We used the number of consecutive incubation days that yielded the best performance for nest detection in step *vi* and calculated recall estimates as cross-validation tests (see below).

Results

Using ODBA data to determine the timing of incubation shifts (i)

Initially, we assessed if ODBA records at 10-min intervals could accurately indicate when male and female sandgrouses incubate. Differences in the timing of morning (*mShift*) and evening (*eShift*) shifts between females and males were near zero and most non-zero outcomes exhibited small positive morning and negative evening differences (see Fig. S2, Additional File 1). These results align with our initial expectations, as male morning shifts should line up or slightly precede female morning shifts, and female evening shifts should line up or slightly precede male evening shifts. For *mShift* differences ($n = 83$), 61.4% indicated a maximum interval of 14 min, and 79.5% of 28 min. Similarly, 43.9% of *eShift* differences ($n = 98$) showed a maximum interval of 14 min, and 73.5% of 28 min. Longer intervals (> 28 min) were also observed for both morning (19.3% *mShift* differences) and evening shifts (25.5% *eShift* differences), albeit less frequently. These results showed that ODBA data collected at 10-min intervals reliably detect the approximate time of incubation shifts and identify when male and female sandgrouses incubate.

Determining sex-specific incubation windows (ii)

Next, we determined sex-specific incubation windows that allowed for a clear distinction between incubation and non-incubation days. Initially, we analysed the consistency and variation of shift timings across the breeding season, obtaining intermediate repeatability scores (R) for both morning (mean ± SD of 0.54 ± 0.05; CI [0.42, 0.63]; $P<0.001$) and evening (mean ± SD of 0.52 ± 0.05; CI [0.41, 0.61]; $P<0.001$) shifts. As expected, this suggests that shift times are more consistent within clutches than between clutches, even when more than one clutch is from the same individual. Therefore, to address the variation in shift times, window limits were estimated considering the average differences between *mShifts* and sunrise time (03:20 ± 00:45H) and between sunset time and *eShifts* (00:52 ± 00:40H).

Afterwards, we analysed daily ODBA patterns of each sex across different breeding stages to identify timeframes when variations in ODBA levels between nesting and non-nesting stages were more pronounced. As shown in Fig. 3A, B (see also Fig. S3, Additional File 1), both sexes had comparable ODBA patterns throughout non-nesting periods (also corresponding to the behaviour of non-breeding individuals), showing minimal activity (low ODBA values) at night, when they roost, and activity peaks between sunrise and mid-morning, and before sunset. Additionally, both sexes reduced their activity from mid-morning to evening (Fig. 3A, B). ODBA patterns confirmed that males engage in incubation duties close to sunset, remaining on the nest until mid-morning, whereas females start to incubate at mid-morning and continue on the nest until evening (Fig. 3A, B). In contrast, ODBA patterns obtained when sandgrouses were out of the nest were similar to those observed during non-nesting periods (Fig. 3A, B). Overall, differences in ODBA levels between nesting and non-nesting periods were more pronounced around sunrise for males and around mid-day for females (Fig. 3A, B).

Repeatability tests revealed consistent but still variable shift timings. Taking these into account, we established a 2-h window for males relative to sunrise (Δ = [sunrise−0.5 h; sunrise + 1.5 h]; see Fig. 3A) and for females centred around mid-day (Δ = [mid-day−1 h; mid-day + 1 h]; see Fig. 3B). Consistent with the

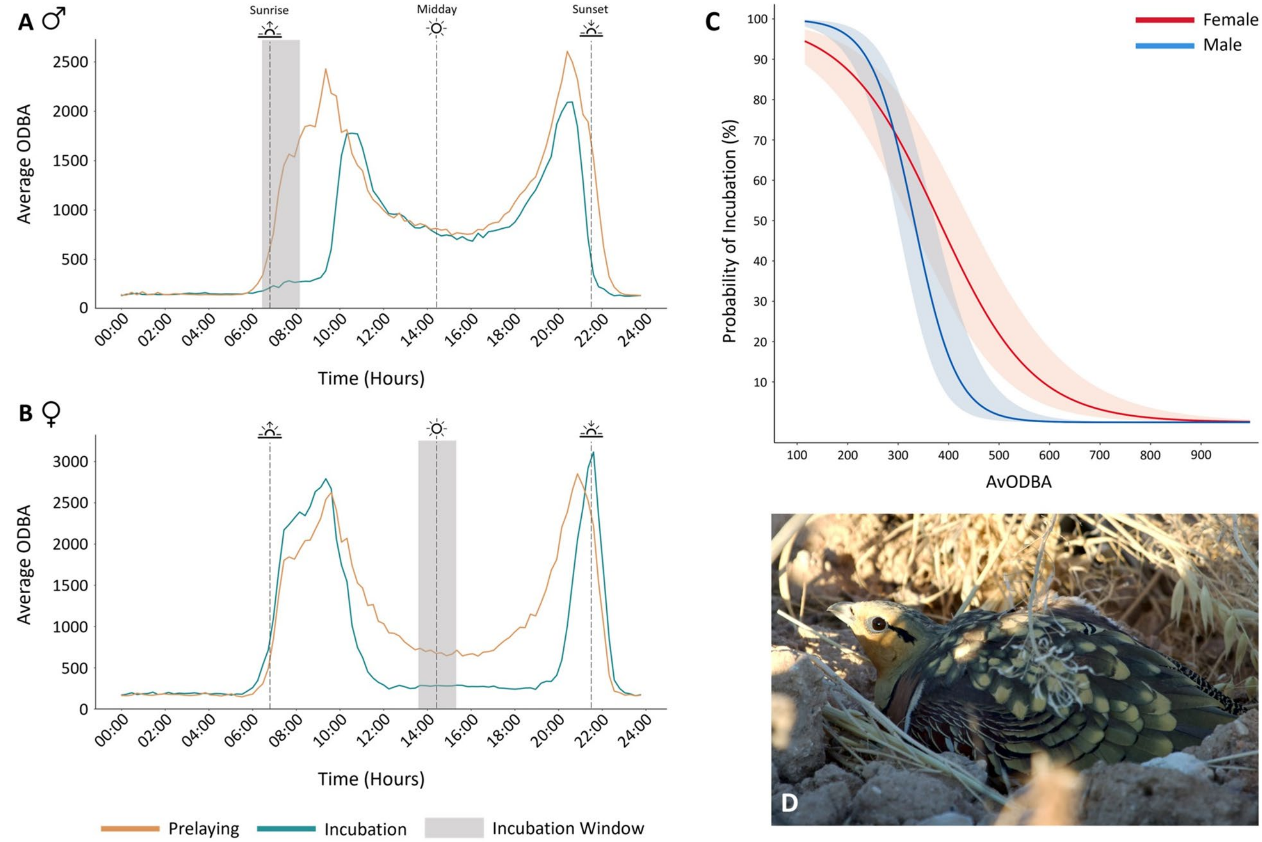

Fig. 3 Daily ODBA patterns, male (**A**) and female (**B**) incubation windows, and incubation probability–AvODBA relationship (**C**). Daily ODBA patterns during prelaying and incubation are illustrated for male (**A**) and female (**B**) sandgrouses. The vertical grey bars show the 2-h incubation windows selected for males near sunrise and for females centred around mid-day (see also Fig. S3, Additional file 1). The response curve (**C**) shows the sex-specific relationships between the probability of incubation and AvODBA during the selected incubation windows. Image **D** illustrates a male pin-tailed sandgrouse incubating early in the morning (photo credit: F. Mougeot)

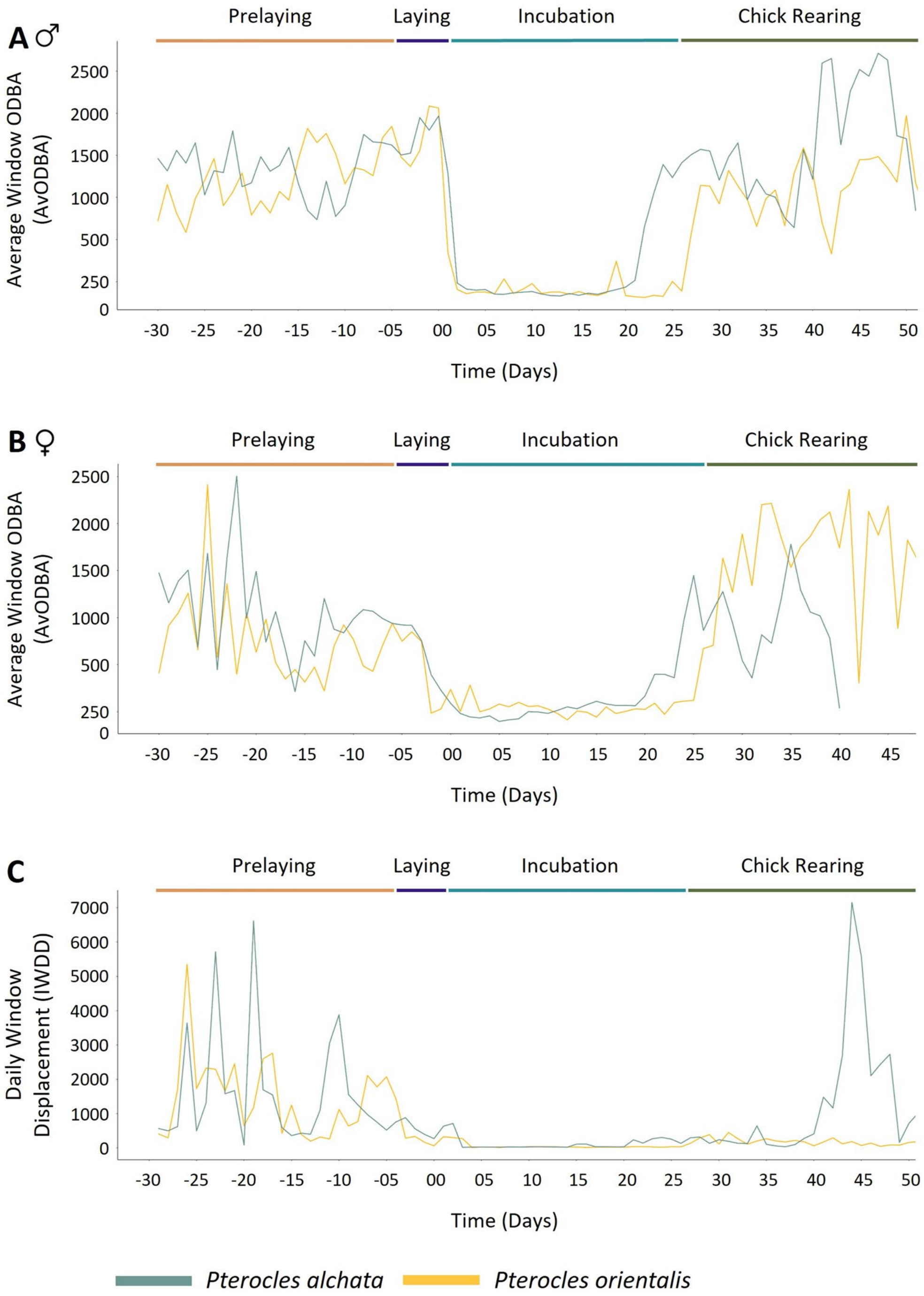

Fig. 4 Daily variations in window AvODBA (activity) and IWDD (movement), relative to incubation onset (day 1). Breeding stages (prelaying, laying, incubation, and chick rearing) are indicated on top of figures. AvODBA values are presented for males (**A**) and females (**B**) of each species separately, to highlight differences between sexes. IWDD values (**C**) are presented for each species in metres. Note that the duration of the incubation period differs between species (green: *Pterocles alchata*, PTS; yellow: *Pterocles orientalis*, BBS)

observed differences between nesting and non-nesting periods, the distribution of AvODBA values calculated during each sex's window confirmed that the selected windows allowed for a clear differentiation between both stages (Fig. 4A, B). Differences were more pronounced for males than females (Fig. 4A, B) because sandgrouses have reduced activity levels at mid-day, even during non-nesting stages (Fig. 3B; see also Fig.

S3, Additional File 1). The distribution of distances moved between the average window location and that of the previous day (IWDD; Fig. 4C) also indicated a clear differentiation between nesting and non-nesting stages, with nesting individuals showing low displacement values while on the nest.

Determining ODBA thresholds (iii)

We used AvODBA values, calculated during sex-specific incubation windows, to determine incubation thresholds that allow to discriminate between incubation and non-incubation days. The relationship between incubation probability and AvODBA did not differ between species (GLMM; $X^2 = 0.0435$; $df = 1$; $P = 0.83$) but differed between sexes ($X^2 = 17.21$; $df = 1$; $P < 0.001$; Fig. 3C). We thus determined sex-specific AvODBA threshold values for incubation probabilities of 0.70 (296 for males and 302 for females), 0.75 (286 for males and 278 for females), and 0.80 (274 for males and 251 for females).

Table 1 Performance metrics of different AvODBA threshold values in identifying incubation days

P Incubation	*Pr* (%)	*Rc* (%)	*MsD* (%)	*F-Score* [0–1]
0.70	74.11	85.25	10.53	0.79
0.75	77.02	83.33	9.82	0.80
0.80	80.64	76.23	9.95	0.78

Performance indicators include precision (*Pr*), recall (*Rc*), proportion of misclassified days (*MsD*) and *F-Scores* for AvODBA thresholds and incubation probabilities (*P* Incubation) of 0.70, 0.75, and 0.80. Values correspond to the whole data set (females + males). Results are provided by sex in Table S3, Additional File 1

Framework's performance to identify nesting events (v–vi)

To evaluate the framework's (Fig. 2) capacity to detect nesting events, we initially followed a three-stage process. First, we evaluated the efficiency of AvODBA thresholds for incubation probabilities of 0.70, 0.75, and 0.80 in correctly identifying incubation days. The best model (with lower *MsD* and higher *F-Score,* maximising the balance between precision and recall) used an incubation probability of 0.75 (AvODBA thresholds of 278 for females and 286 for males; Table 1). While a similar performance was observed for females, we found a consistent performance for males across all incubation probabilities (see Table S3, Additional File 1). When comparing both sexes, the model performed better for males than females. Further validation steps were performed using sex-specific AvODBA values at 0.75 incubation probability.

Second, we evaluated the capacity of ODBA-only, GPS-only, and combined GPS–ODBA data in detecting incubation days. Analyses with the complete data set (females + males) showed that ODBA-only data

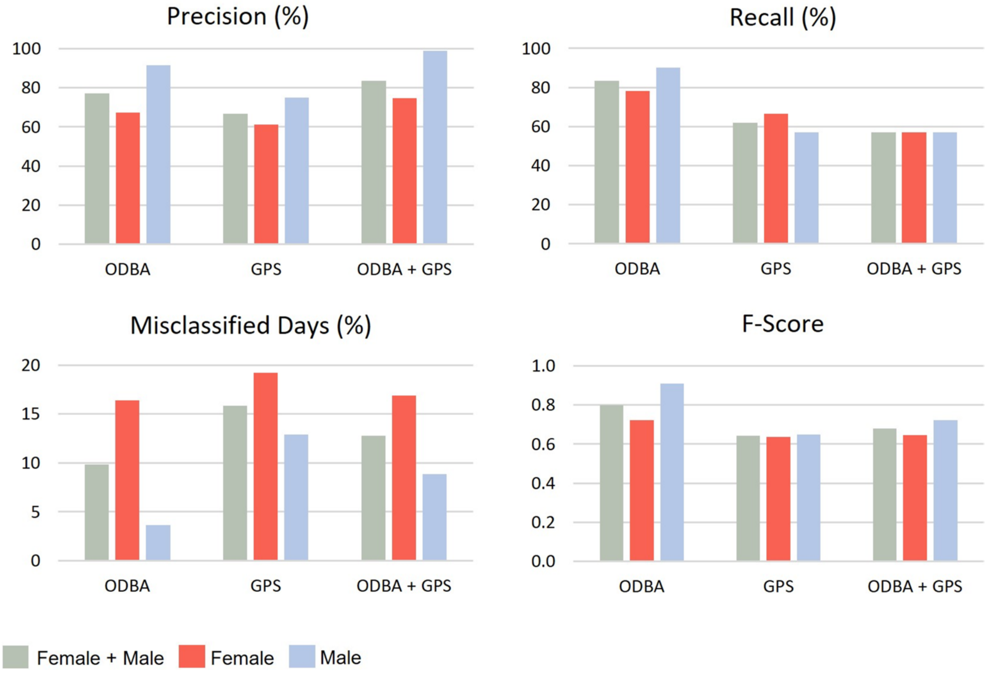

Fig. 5 Statistical evaluation of the framework's performance in detecting incubation days using different types of data. Estimates of precision (*Pr*), recall (*Rc*), misclassified days (*MsD*) and *F-Scores* were obtained for each type of data (ODBA-only data, GPS-only data or combined GPS–ODBA data) using the whole data set (females + males) and data from each sex separately

performed better to detect incubation days (higher *F-Scores* and lower *MsD;* Fig. 5). Results obtained for the combined GPS–ODBA data were similar, but slightly better, than those obtained for GPS-only data (Fig. 5), with higher *F-Scores* and lower *MsD* estimations (Fig. 5). When looking at the framework's performance by sex, incubation days were generally better identified for males than females (Fig. 5). For both sexes, ODBA-only data performed better than GPS-only data or combined GPS–ODBA data (Fig. 5). Combined GPS–ODBA data performed better than GPS-only data for males (higher *F-scores* and lower *MsD*), but both yielded similar *F-scores* for females, although the first had lower *MsD* estimations (Fig. 5).

As a third step, we assessed the framework's ability to detect nesting events. Since nests are identified only when AvODBA and/or IWDD values fall below specific thresholds for a minimum number of consecutive days (Fig. 2), the performance of each data type was evaluated over time periods ranging from 2 to 7 days (Fig. 6; see also Fig. S4, Additional File 1). The 3-day period performed the best for ODBA-only and GPS-only data for males and females, with higher *F-Scores* (ODBA = 0.92; GPS = 0.82) and lower *MsP* estimates (ODBA = 5.94%; GPS = 13.49%). By contrast, the 2-day period had a better performance with combined GPS–ODBA data (*F-score* of 0.91; *MsP* of 6.93%; Fig. 6). Similar *F-Scores* were also obtained for ODBA-only and GPS-only data when using 2- and 4-day periods, although both yielded larger *MsP* estimates, with the first showing more false positives and the latest more false negatives (Fig. 6; see also Fig. S4, Additional File 1). Performance dropped when using longer periods (5–7 days). Overall, ODBA-only data and combined GPS–ODBA data had similar performances when using 2- and 3-day incubation periods, outperforming the results of GPS-only data (Fig. 6; see also Fig. S4, Additional File 1).

The framework's performance to detect nesting events also differed between sexes (Fig. 6; see also Fig. S4, Additional File 1), working generally better for males than females when using 2- or 3-day periods (higher *F-scores* and lower *MsP* estimates). While for males ODBA-only data successfully detected all nests after only 2 days of incubation (*F-score* of 1), for females we observed a higher *F-score* using a 3-day period (*F-Score* of 0.89). By contrast, GPS-only data performed the best for both sexes when using a 3-day period, although it performed the least both for males (*F-score* of 0.87) and females (*F-score* of 0.79). Combined GPS–ODBA data achieved an intermediate performance for males when using 2- or

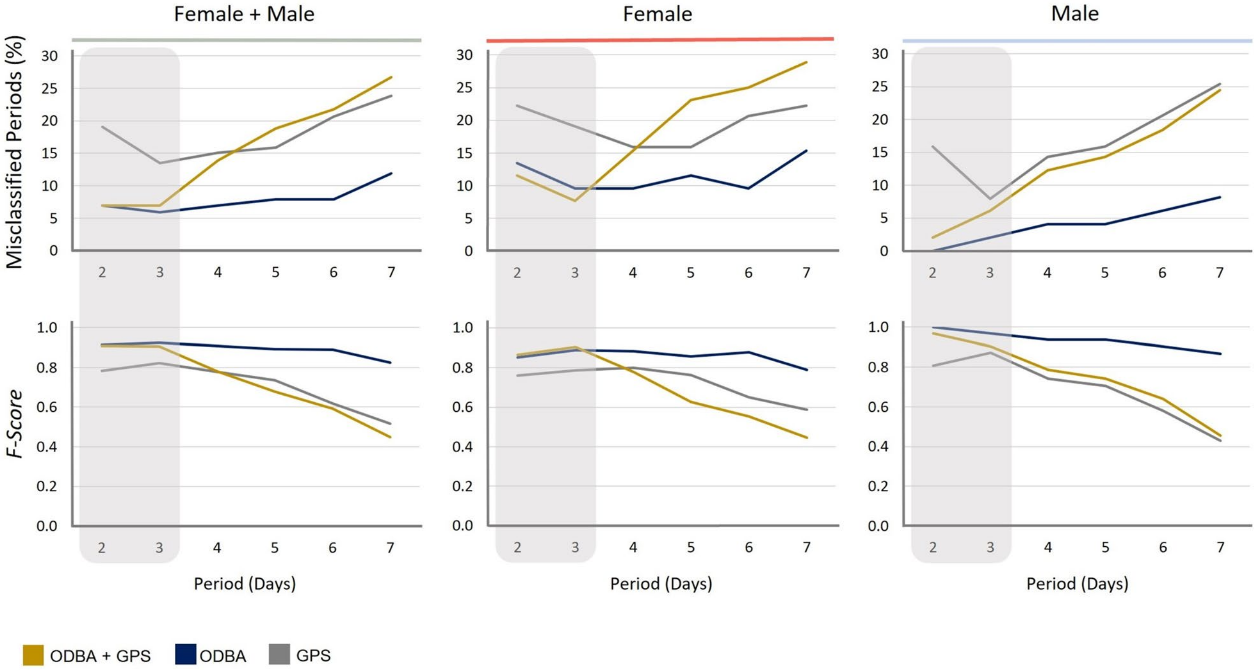

Fig. 6 Framework's performance for detecting nesting events across different time windows using ODBA and/or GPS data. The proportion of misclassified breeding events (or periods; *MsP*) and *F-Scores* were calculated for ODBA-only data, GPS-only data, and combined GPS–ODBA data using the whole data set (females + males) or data from each sex separately. The best periods to determine nesting events (2 or 3 consecutive days with positive detection of incubation) are highlighted in grey. Complementary data on precision (*Pr*) and recall (*Rc*) estimates are shown in Fig. S4, Additional File 1

3-day periods and worked better after only 2 days of incubation (*F-score* of 0.97; Fig. 6; see also Fig. S4, Additional File 1). For females, combined GPS–ODBA data outperformed ODBA-only and GPS-only data when using 2- or 3-day periods, with higher *F-scores* (0.86 and 0.90 for 2- and 3-day periods, respectively) and lower *MsP* estimations (11.54% and 7.69% for 2- and 3-day periods, respectively). Finally, model performance dropped for both sexes for longer time periods (4–7 days; Fig. 6; see also Fig. S4, Additional File 1).

Cross-validation (vii)

When testing our framework using an independent set of sandgrouse nesting attempts, we obtained high recall estimates using the 2-day incubation period: the framework accurately detected 91–95% of nests when using ODBA-only or GPS-only data and 85% of these when using combined GPS–ODBA data (Table 2). Recall estimates were similar between the training data set and the test data set using a 2-day period for GPS-only data but dropped by 9% for ODBA-only data or combined GPS–ODBA data. Larger differences were observed when using a 3-day period, mainly due to an increase in false negatives (Table 2; Fig. S4, Additional File 1).

Discussion

We have developed and validated a framework that successfully identified sandgrouse nesting events after only 2–3 days of incubation with a high level of precision and sensitivity. This is new and significant because it enables research on the breeding biology of cryptic and elusive ground-nesting species, such as sandgrouses, reducing disturbances associated with nest searching or visits. By remotely monitoring nesting events and better scheduling potential nest visits, researchers are not only able to reduce the impacts of fieldwork on breeding outcomes, but also expenses associated with field logistics and enhance safety around areas of special conservation concern [26]. To the best of our knowledge, this study is the first to simultaneously evaluate the performance of GPS-only data, ODBA-only data, and combined GPS–ODBA data in detecting nesting attempts in bird species with biparental care and alternating incubation schedules, complementing the methodologies proposed previously for species with uniparental care and prolonged nest attendance [20, 32]. Below, we discuss how the framework and biologging data collection can be optimised and successfully applied to other species.

Table 2 Recall estimates obtained when applying the framework to the cross-validation data set

Type of Data	2 days	3 days
ODBA	91.18	79.41
GPS	95.24	90.48
ODBA + GPS	85.29	64.71

Recall estimates, representing the percentage of correctly identified nests, were obtained by applying the proposed framework to the cross-validation data set (see step *vii* and Table S2, Additional File 1). For GPS-only data, the analysis was based on an initial set of 42 nests, while for ODBA-only data and combined GPS–ODBA data we used a set of 34 nests. All nests included in this step were remotely detected and field-validated during 2023–24

Identifying nesting events using GPS and ODBA

We expected that biologging data would discriminate between incubating and non-incubating birds, based on the assumption that sandgrouses exhibit minimal body motion (low ODBA) and mobility (GPS positions showing no displacement) while on the nest. To account for daily variations in nest attendance between sexes, which had not been considered in previous studies [20, 32], we first identified and limited daily records to sex-specific time windows defined by each sex incubation schedule. This approach maximised differences between incubation and non-incubation periods, which was particularly important to identify possible incubation days, and consequently, nesting events as a minimum succession of possible incubation days.

Model performance

The approach developed by Schreven et al. [20] allowed to identify nesting attempts with a resolution of 3 days of incubation using combined GPS–ODBA data (98.1% success rate). The methodology proposed by Ozsanlav-Harris et al. [32] obtained similar results ($Rc > 98\%$) not only with combined GPS–ODBA data but also using GPS-only data. Schreven et al. [20] did not estimate success rates using ODBA-only data, and Ozsanlav-Harris et al. [32] highlighted that ODBA-only data would perform the least well. In our study, the developed framework was highly successful in detecting nesting events, achieving an overall success rate (recall) over 90% after just 2 days of incubation when using either ODBA-only data or GPS-only data and 85% when using combined GPS–ODBA data. ODBA's capacity to discern daily activities based on differences in activity-specific metabolic rates [20, 29, 52] allowed for improved discrimination between incubation and non-incubation days in both sexes compared to GPS-only data or combined GPS–ODBA data. Despite lower recall estimates during cross-validation, ODBA-only data proved to be effective in distinguishing nesting from non-nesting activities and identifying sandgrouse nesting events. When using a 2- or 3-day period, ODBA-only data provided low misclassification rates and high *F-scores*, identifying over 97% of all nests considered in the training data set. When comparing the performance between sexes, ODBA-only data was able to accurately identify all nesting attempts after only 2 days of incubation for males and 3 days for females.

Conversely, performance tests revealed that, despite yielding higher recall estimates during cross-validation, GPS-only data performed the least effectively overall, either for males or females. GPS-only data successfully detected nesting attempts because of immobility during incubation (e.g., [20, 26, 31, 32]). However, in our study, it resulted in more days flagged as false positives or false negatives, lower *F-Scores,* and more misidentified nesting events. Despite these limitations, GPS-only data successfully identified 95.5% and 95.7% of the nests included in the training data set for males and females, respectively, when using a 2-day period. When using a 3-day period, GPS-only data identified 77.3% of male nests and 95.7% of female nests. Although the 3-day period provided higher recall estimates for females, it had low precision (more false positives; 66.67%), leading to a lower *F-score* compared to males.

Ultimately, the effectiveness of combined GPS–ODBA data to identify nesting days depended on their ability to accurately identify days of incubation. Combined GPS–ODBA data provided an overall intermediate performance, with an *F-Score* comparable to ODBA-only data but lower recall estimates (confirmed during cross-validation). Additionally, performance varied between sexes. In males, ODBA's strong capacity to identify nesting days, alongside the more limited capacity of GPS-only data, resulted in an intermediate performance, while for females, the poorer capacity of GPS-only and ODBA-only data led to more misclassified days compared to using ODBA-only or GPS-only data. Nonetheless, around 70% of the days flagged as possible incubation days either by ODBA-only (65.06%) or GPS-only (69.72%) data were flagged as possible incubation days when combining both. While for males combined GPS–ODBA data resulted in an intermediate performance (94.1% of the nests detected when using a 2-day period), for female sandgrouses it provided a better balance between precision and recall (higher *F-score*), detecting 95% of the nests. Despite differences in performance between types of data and sexes, we achieved a temporal resolution comparable to previous works [16, 20, 32], successfully detecting nests after only 2 or 3 days of incubation for both males and females.

Variations in model performance between sexes when using ODBA-only data were primarily linked to differences in window activity levels during nesting and non-nesting days. While larger differences in male activity resulted in lower misclassification rates, we observed a more gradual variation for females, likely due to periods of reduced activity during the incubation window, centred around mid-day, on non-nesting days. As a result, we found more days misidentified as incubation days (78 false positives for females and 13 for males). Defining threshold values that better suit variations in activity levels could potentially improve the accuracy of the framework when using ODBA-only data, particularly in cases where there is a smoother transition in activity between incubation and non-incubation periods, as observed for females. Furthermore, future research could investigate whether temperature data from biologging devices could improve model performance, as steppe birds might be less active under warmer conditions [53, 54], particularly after mid-day, and activity level differences between nesting and non-nesting days should be greater when temperatures are lower. GPS patterns during incubation were expected to be similar between sexes, with variations in performance attributed to revisits to roosting or feeding locations or differences in the inherent spatial error of each device. By not differentiating nesting from non-nesting behaviours, GPS-only data was not capable of efficiently discerning between revisits to nest sites or to roosting or feeding locations, at least when limiting daily records to incubation windows. Finally, by considering both low mobility and minimal body motion, combined GPS-ODBA data enhanced our ability to identify incubation behaviour. We found this combination to be particularly effective when neither ODBA-only nor GPS-only data allowed for a clear differentiation between nesting and non-nesting days, as observed for female sandgrouses.

Framework and data collection optimisation

Unlike previous works that identified nesting attempts considering ODBA and GPS data collected throughout the day [20, 32], we limited our assessment to predetermined incubation windows within each sexes' incubation schedule. To get the optimal window for each sex, we needed a previous understanding of the breeding biology of the species of interest, acknowledging which sex incubates and at which time of the day (e.g., [17, 36, 43]). Although the selection of incubation windows might not be a challenge for species with uniparental care, it may be more difficult for species with biparental care, particularly those with less available information on nest attendance schedules.

Although we collected data at frequencies (GPS at 20- or 30-min intervals and ODBA at 10-min intervals) that were previously shown to be efficient for nest detection [32], we recognise that limiting records to specific time windows may pose a challenge, particularly when data is collected at larger intervals, and that data frequency could be adjusted to increase data collection during the time window to improve model performance. Despite the rapid evolution of tracking technologies over the last decades, the miniaturisation of tracking devices remains one of the main constraints to its application in smaller species [55]. While previous works have achieved high performance for nest detection using heavier devices that accommodate larger batteries and are capable of collecting data at higher frequencies over extended periods (38 g Ornitela tags; ACC at 6 to 10-min intervals and GPS at 10–15-min intervals; [20, 32]), in this study, we were limited by the sandgrouse's smaller size, selecting devices that allowed us to find the best balance between tag weight and sampling frequency. Specifically, devices deployed in this study (5 to 6 g Druid mini tags and 9 g Ornitela tags) were below the threshold of 2% of body weight [56] and allowed data collection at a temporal scale sufficient to ensure high-quality data and long-term device performance [57].

While ODBA-only data proved highly effective in identifying nesting events when narrowed to a 2-h window (maximum of 12 ODBA readings per window), we encountered challenges in assessing its performance for birds tagged with Ornitela tags. This was primarily due to differences in the frequency of data collection between the two tags (ACC readings at 20-min intervals for Ornitela) and day/night settings that reduced data collection during the night, limiting analyses during the male window. On the other hand, GPS-only data had the lowest performance for nest detection, possibly due to the lower GPS precision determined for Druid devices (31 m error) and fewer records within the incubation windows (maximum of four records per window for Druid tags and six for Ornitela). While Druid tags were already configured for best battery management aiming for long-term viability of the logger, our results showed a posteriori that we could have improved the settings of Ornitela tags to increase the frequency of data collection during the incubation windows of males and females. Additionally, Ornitela tags could be configured to optimize data collection according to battery levels, as performed in Schreven et al. [20], allowing for better management of the logger's long-term performance. Given these limitations and potential solutions, for future applications of the framework we suggest the selection of devices that enable improved data collection during incubation windows, with battery management when collecting ODBA or ACC data at high temporal intervals such as 10 min or less and GPS data at intervals of 10 or 15 min [16, 20, 32]. To enhance the performance of GPS-only data or combined GPS–ODBA data, we recommend adjusting window length and the number of GPS fixes according to pre-determined GPS error estimates. Finally, special care should also be given to the position of the tag on the individual, as it could impact the sensitivity of the accelerometer depending on the species.

Finally, our approach should be complemented with fieldwork to fully understand the outcome of each nesting attempt and accurately estimate breeding parameters, such as hatching success, crucial for the conservation of the species under study. Sandgrouse are nidifugous, making nesting success or fledging success very challenging to determine remotely without field validation. Still, the detection of nesting events after 2–3 days of incubation provides very valuable information on their reproduction without the need to visit nests during incubation.

Remote tracking as a tool to study the reproduction of inconspicuous and sensitive species

Assessing the breeding performance of wild birds may be particularly difficult for species that are cryptic, ground-nesting or sensitive to human disturbances, such as sandgrouses, as nests are often not visible from a distance, and field work to locate them could both impact breeding outcomes and be biased to habitats or locations that enhance nest detectability [17, 25, 58, 59]. Without remote tracking of tagged individuals, researchers have a limited capacity to study breeding performance, estimate nest survival, productivity, or the general factors influencing breeding success [16, 20, 32]. Given the need to overcome these limitations, our framework, complementary to the works of Schreven et al. [20] and Ozsanlav-Harris et al. [32], relies on high resolution GPS and ODBA data to remotely detect nesting events with high precision. It enables researchers to identify nesting events even if they fail early in incubation and get a better understanding of the factors that may affect breeding success.

While primarily designed for ground-nesting species with biparental efforts during incubation, the proposed methodology has a broader scope and may be applied to other species. Characterised by discrete incubation windows and predetermined thresholds, our methodology not only distinguishes nesting from non-nesting behaviours in biparental species but also shows potential utility for those with uniparental care (e.g., [60]) or with inaccessible nest sites (e.g., [61, 62]), if the roles of each sex during incubation and the temporal patterns of nest attendance are distinguishable (e.g., [28]).

However, we recognise the need for caution when applying it to other species to ensure that tracking devices do not interfere with breeding outcomes. Biologging may inadvertently interfere with breeding success, potentially limiting nesting capacity and increasing energetic expenditure (e.g., [63–65]). For example, studies with thick-billed murres (*Uria lomvia*; [64]) and little auks (*Alle alle*; [65]) revealed that tagged individuals experienced body mass loss and prolonged foraging trips, ultimately reducing chick provisioning. Furthermore, untagged mates were also affected, as they had to compensate for the reduced offspring attendance. Therefore, careful consideration must be given to the potential impacts of tracking methods on breeding dynamics before their implementation.

Conclusion

This study highlights the great potential of high-resolution GPS and ODBA data to identify nesting events. In our model species, both sexes shared incubation duties, so we had to determine sex-specific incubation windows that enabled us to better discriminate between incubation and non-incubation days, and then used a threshold-based framework to precisely identify nesting events in both sexes. Cross-validation showed that ODBA-only and GPS-only data achieved a success rate over 90%, while combined GPS–ODBA data had a success rate superior to 85%. We acknowledged some limitations of our approach and proposed potential solutions to further enhance its performance and applicability to species with biparental or uniparental care. While further research is necessary to refine the approach, biologging offers new opportunities to remotely obtain information on key demographic parameters, such as dispersal, survival, and breeding performance, that are crucial for the conservation of inconspicuous or sensitive species.

Abbreviations

ACC	Acceleration
GPS	Global positioning system
IWDD	Incubation Window Daily Displacement
ODBA	Overall dynamic body acceleration

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-024-00385-y.

Additional file 1: Using GPS and accelerometer data to remotely detect breeding events in two elusive ground-nesting steppe birds. Additional File 1 shows texts, tables and figures that supplement the information provided both in the Methodological and the Results sections

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Author contributions

GF, FM and JPS conceived the idea for the project. CP, FM, JPS and GF collected the data. GF, MFT, FM and ATM analysed the data. GF, FM and JPS wrote the initial manuscript. JPS and PCA acquired funding. FM, JPS and PCA supervised research. FM and JPS equally supervised and contributed to the manuscript. All authors contributed to the edition of the manuscript and approved its final version.

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Availability of data and materials

The datasets generated and/or analysed during the current study are not publicly available due to the sensitivity around the locations of these breeding birds and the current use for further unpublished works but are available from the authors upon reasonable request.

Declarations

Ethics approval and consent to participate

The capture, handling and tagging of black-bellied and pin-tailed sandgrouses was performed in compliance with *Instituto da Conservação da Natureza e Florestas* (ICNF), the Portuguese national authority regulating nature conservation (permit no 378 / 2021 / CAPT), the Spanish Autonomous Community of Extremadura (permits no CN0017/21/OT; CN0006/22/ACA; CN0075/22/ACA; and CN0003/24/ACA) and with the necessary experimentation permits for Spain (certificate number CAP0700374, JCCM).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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