FROM PRACTICE

Ecological Solutions and Evidence | BRITISH ECOLOGICAL SOCIETY

Using UAV-mounted thermal cameras to detect the presence of nesting nightjar in upland clear-fell: A case study in South Wales, UK

Mike P. Shewring[1,2] | **Jim O. Vafidis**[3]

[1] School of Biosciences, Cardiff University, Cardiff, UK

[2] MPS Ecology, Heol y Cyw, Bridgend, UK

[3] Department of Applied Sciences, University of the West of England, Bristol, UK

Correspondence
Mike P. Shewring, School of Biosciences, Cardiff University, Cardiff, CF10 3AX, UK.
Email: shewringmp@cardiff.ac.uk

Handling editor: Rachel White

Abstract

1. Confirming the presence and location of European Nightjar *Caprimulgus europaeus* nests is a significant fieldwork challenge in ecological monitoring. Nest sites can be located through direct observation or capture and radio tracking of breeding individuals; however, such work is time consuming, disturbing and costly.

2. Unmanned aerial vehicles (UAV) equipped with thermal sensors may enable rapid survey over large areas by detecting nest locations based on the contrast of relatively warm nests and the surrounding cooler ground. The application of this concept using UAV-mounted thermal sensors was trialled in two upland clear-fell forestry sites in South Wales, UK.

3. Detection trials were undertaken at five known nightjar nest sites to assess optimal timing and flight height for surveys. Nest heat signatures were clear during dusk and dawn, but not during the daytime. Nests were identifiable at flight heights up to 25 m, but flight heights of 12–20 m were optimal for the numbers of pixels per nest.

4. This approach was tested in a field trial of a 17-ha forestry site where the presence and position of nesting nightjars were unknown. An automated transect at dusk and dawn at 15 m flight elevation identified two active nightjar nests and four male nightjar roost sites. Without image analysis automation, the process of manual inspection of 2607 images for 'hotspots' of the approximate size and shape of nightjar nests was laborious.

5. The UAV approach took around 18 h including survey time, processing and ground verification, whilst a nightjar nest finding survey would take 35 h for the same area. The small size of nightjars and the low resolution of the thermal sensors requires low altitude flight in order to maximize detectability and pixel coverage. Low flight elevation requires more consideration of the risk of collision with trees or posts. Consequently, the approach would not be suitable for covering areas of highly variable terrain.

KEYWORDS
drone, nests, nightjar, remote sensing, UAV

---

1 | INTRODUCTION

The identification of breeding sites of cryptic species, such as European Nightjar *Caprimulgus europaeus* (henceforth nightjar), is a significant challenge for population monitoring, especially where such species are of conservation concern. Nightjar are a predominantly ground-nesting species that typically lay two eggs (occasionally one egg) and usually produce two broods per breeding season, with nests mostly attended by the female during the day and by both adults at night, the nesting cycle is usually completed over approximately 36 days (Holyoak, 2001). Nest locations of this sub-Saharan migrant are difficult to identify due to their cryptic camouflage (Troscianko et al., 2016), crepuscular behaviour and low nesting densities across large areas (Cross et al., 2005; Holyoak, 2001). As such, crypsis can mean lower confidence in population estimates and uncertainty in the regional presence or absence of breeding individuals (Couturier et al., 2013; Ward et al., 2017).

Nightjar are a species of conservation concern (Amber listed in the United Kingdom; Eaton et al., 2015) and known to be sensitive to disturbance during the breeding season. Disturbance can have a negative impact on breeding success due to direct damage through trampling or through increased rates of egg predation due to exposed nests after flushing adults (Langston et al., 2007; Liley & Clarke, 2003; Lowe et al., 2014; Murison, 2002; Rayner, 2016). The potential negative effects of disturbance from anthropogenic activities mean that forestry, infrastructure and construction organizations regularly face delays and restrictions to activities due to the presence of protected species, such as nightjar, in areas of operation (Shewring & Carrington, 2015). This can lead to a requirement for time-consuming and specialist survey work as well as restrictions on the timing and location of planned work, where legally protected features are likely or confirmed (Shewring & Vafidis, 2017).

Technological innovations that may increase detection probability and thus minimize the impact of crypsis abound (e.g. radio tags: Alexander & Cresswell, 1990; thermal imagery: Boonstra et al., 1995; Boulton & Cassey, 2012; Galligan et al., 2003; McCafferty et al., 1998; and recently the use of unmanned aerial vehicles [UAVs]). UAV-mounted thermal sensors can monitor the heat radiation of visually cryptic endothermic animals to identify their location (Bushaw et al., 2020; Israel & Reinhard, 2017; Santangeli et al., 2020; Seymour et al., 2017; Witczuk et al., 2017;). UAVs can provide a means of rapidly surveying large areas using thermal sensors and may represent a more cost-effective less disturbing alternative to traditional research methods (Bushaw et al., 2020; Christie et al., 2016; Santangeli et al., 2020).

A key issue in the use of UAV-mounted thermal technology for wildlife applications is the optimization and confidence in detection probability. Detection probability can be affected by the time of day but also by the ambient conditions and flight characteristics – speed and flight altitude (Witczuk et al., 2018). The probability of false absences is also known to be more likely when images are taken from further above ground level (Santangeli et al., 2020), suggesting flight height above the ground is a key consideration in conservation applications.

Field applications using UAVs are not without their risks to ground-nesting birds, and disturbance responses have been recorded in some species (Bevan et al., 2018; Weimerskirch et al., 2018). A recent review by Mulero-Pázmány et al. (2017) noted that target-oriented flight patterns, larger UAVs sizes and noisier (fuel-powered) engines evoked stronger disturbance responses from animals and that birds were more likely to react than other taxa. Weimerskirch et al. (2018) noted significant approach distance effects, with distances <10 m provoking responses in the majority of breeding Antarctic bird species studied, whilst Bevan et al. (2018) noted a direction of approach effect with vertical approaches the most likely to result in disturbance at a colony of breeding crested tern (*Thalasseus bergii*). Work by Weston et al. (2020) identified not only approach distance but also proximity of take-off location as a key factor in the response of a species. Whilst work by McEvoy et al. (2016) also identified the shape of the UAV (e.g. raptor like or novel etc.) as an important factor.

In this article, we report on an opportunistic project to investigate the use of UAV-mounted thermal sensors to detect nightjar nests at two upland field sites under active land management in South Wales, UK. The study includes nest detection trials in which known nightjar nest sites are used to achieve objectives of (1) comparing nest-ground temperature differences between dawn, midday and dusk; (2) investigating the effect of flight altitude on nest detectability. This study then uses a field trial in which a UAV survey protocol, informed by 1 and 2, is used to (3) test if unknown nightjar nests can be located.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was undertaken at two field sites in South Wales, UK; Bryn Forest ('Bryn', SS 820 903) in Neath Port Talbot; and Cwmcarn Forest ('Cwmcarn', ST 230 928) in Caerphilly (Figure 1). Bryn is located between 200 and 350 m above sea level (asl) whilst the Cwmcarn study area spanned 350–380 m asl. Both field sites are owned by the Welsh Government and managed by Natural Resources Wales as part of large (>100 ha) forestry sites with continuous plantations of Sitka spruce (*Picea sitchensis*) and Norway spruce (*P. abies*) and large areas of clear-fell.

In Bryn, five nightjar nest sites with known positions and developmental statuses were investigated. These nests were located using a combination of field observation and radio tracking by the authors as part of ongoing conservation monitoring and scientific research. At the time of the study, three nests were at the egg stage, and two nests were at the chick stage. The exact position of nests was recorded as GPS locations and marked discretely in the field using orange flagging tape on adjacent vegetation at 10 m distance.

Cwmcarn is a 17-ha area of recently cleared forestry containing heavily rutted terrain densely covered by forestry brash. This study site represented an area due for immediate brash clearance using a powered forestry mulcher in preparation for new tree planting. At the time of the survey, it was unknown if the area-supported breeding nightjar.
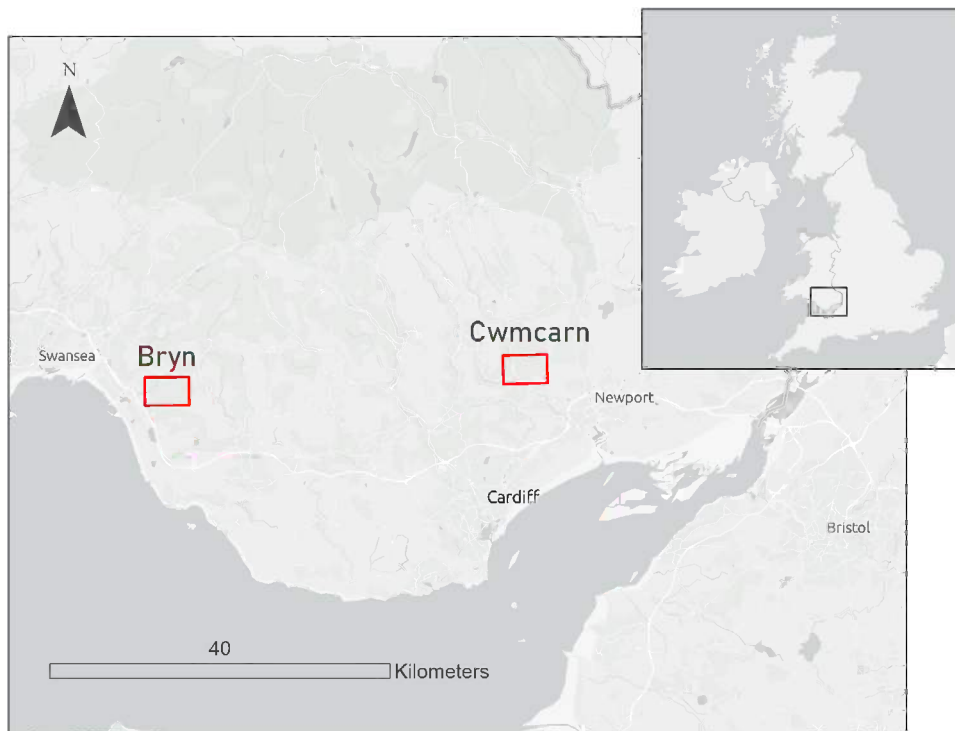
FIGURE 1 Field site locations of Bryn and Cwmcarn in South Wales

TABLE 1 Weather data from closest weather station for dates of survey flights at Bryn and Cwmcarn

Site	Date	Mean temperature (°C)	Mean minimum temperature (°C)	Relative humidity (%)
Bryn	12 July 2018	19.1	16.2	77.3
Bryn	13 July 2018	18.1	15.3	76.2
Bryn	8 August 2018	16.6	14.1	73.7
Bryn	9 August 2018	15.6	12.7	72.2
Cwmcarn	1 July 2019	15.4	11.9	75.1
Cwmcarn	2 July 2019	14.9	10	66.7
Cwmcarn	3 July 2019	16.1	9.8	60.0
Cwmcarn	4 July 2019	17.4	11.8	63.3
Cwmcarn	5 July 2019	17.5	13	67.3
Cwmcarn	6 July 2019	16.9	11.5	77.6

Weather conditions for the relevant flight days were obtained from the nearest weather station (Bryn - <20 km, Cwmcarn - <50 km) using the GSODR (Sparks et al., 2017) package; these data are presented in Table 1.

2.2 | UAV specifications

Two UAVs were used in this study including the Falcon 8 (Ascending Technologies Ltd.) with a gimbal-mounted Tau 640 thermal infrared (IR) camera with 19 mm optics. The Tau 640 has a 640 × 512 pixel resolution and 9 Hz framerate. This was utilized on Bryn in 2018. The study also used a T600 Inspire 1 (DJI Technology Company) with the Zenmuse XT V2.0 FLIR uncooled thermal IR radiometric sensor with a 19-mm lens, 640 × 512 pixel resolution and 30 Hz framerate. This was utilized on both sites in 2019. Both UAVs used in this study were multi-rotor, vertical take-off and landing models.

2.3 | UAV survey

Manual flights at known nest sites utilized a take-off point >100 m from the nest site and followed a high altitude (>50 m above ground level) approach flight. Images were captured at sample altitudes before

returning to flight altitude and returning to the launch point. Default camera settings were used during these flights, and each flight took less than 15 min and was completed on a single battery.

Flight plans utilize a known area of interest as a polygon on a map and calculate a suitable flight path with the requested percentage overlap. Transects were planned and conducted using Pix4D Capture (Pix4D China Technology Company) application running on a Sony Xperia android smartphone. The transect programme involved the image capture of the transect route at 70% overlap (to enable stitching an orthomosaic) and at a 'slow' speed of 1–2 m/s and 90 camera angle. After the UAV launch, the pilot needs to maintain a visual line of sight and needs to intervene only in emergency cases. Each programmed flight was undertaken at a constant velocity with image acquisition at a rate of 1.25 per second. Images were saved on an SD-Card as tagged image file format (tiff) including the GPS position and time. The remote feed from the thermal imaging sensor also enabled real-time detection and monitoring information to the pilot.

2.4 | Nest detection trial

1. To determine whether temperature differences between nests and their environment are significantly different between sample time zones, a total of 79 thermal images of the five nests at Bryn were taken at dawn (0430–0600), midday (1200–1400) and dusk (2030–2200). Mean temperature values were extracted for all nest pixels (manually identified by species specialist – approximately 25 pixels per nest) and surrounding environments (500 randomly selected pixels) to achieve this, temperature values were extracted from each pixel identified as nest pixels or background point pixels, these values were then summed and divided by the number of input pixels. The difference between the two means was calculated for each image by subtracting the environment mean from the nest mean. A linear mixed model (LMM) with an 'identity' link was used to explain the temperature difference using time (dawn, midday and dusk) as a fixed effect. Nest ID was included as a random effect to control for repeated measures on the same nest.
2. To determine the effect of flight altitude on nest detection, 57 thermal images of the five nests at Bryn were collected at altitudes ranging between 5 and 50 m at dusk and dawn. Manually determined nest pixels were counted in each thermal image using the AscTec viewer default colour palette. A LMM with an identity link was used to explain pixel count using flight altitude as a fixed effect and Nest ID as a random effect.

2.5 | Field trial

1. To confirm if nests can be located using UAV-mounted thermal sensors, a transect of all habitats within the boundary of Cwmcarn was undertaken. A total of 17 UAV flights were undertaken between 1 and 6 July 2019 starting approximately 1 h before sunset or dawn and continuing for 40 min after. Each visit involved three flights,

each undertaking a transect survey of an approximately 100 m × 100 m area at a standard flight height of 15 m at launch position. No nocturnal flights were undertaken due to the requirement for visual contact with the UAV for flight safety reasons. Heat signatures in all images were scrutinized for candidate nightjar nests, on the basis of their size (approximately 24 cm long by 10 cm at its widest point) and shape (resting posture; Figures 2–4). The location of all candidate nightjar nests was visited and checked the following day by the authors. These visits included a walkover to the candidate nest location and all suitable nesting habitat within 5 m. Nest sites were confirmed through either the presence of incubating adults, dependent young (chicks) or evidence of the recent presence of adults/young, that is egg shell remains, accumulations of droppings and a nest scrape. Adult roost sites were identified through the presence of either adult birds or an accumulation of droppings in the absence of a nest scrape.

All thermal images were examined for nightjar nests using either AscTec thermal viewer software (2018) or FLIR Tools (2019) using a suitable colour palette (AscTec – default, FLIR Tools -Arctic). The extraction of thermal values and counts of nest pixels were undertaken using ArcGIS Pro 2.5.2 (Esri Inc., 2020). All quantitative data analysis was undertaken in the R statistical software (R core team ,2020) using the lme4 package (Bates et al., 2015) for LMMs. Data exploration and model validation procedures followed Thomas et al. (2017) and consisted of visually inspecting the model residuals for normality and homoscedasticity. Data manipulation and visualization was undertaken using tidyverse (Wickham et al., 2019) and ggplot2 (Wickham, 2016).

2.6 | Disturbance monitoring

The study received ethics committee approval (UWE AWEC R134) with conditions that disturbance to nesting birds be minimized by incorporating a flight approach to each nest by maintaining a smooth consistent movement and not hovering over the nest. During all flights, active nests were monitored through close visual observation by the non-pilot to monitor any disturbance responses to the UAV. In the nest detection trials, this consisted of watching the nest site from a nearby vantage point (approximately 30 m). Beyond the trial, these nests were monitored until their natural conclusion (i.e. completion or failure) following standard nest surveying techniques. During both the field trial and nest detection trial, ground areas in close proximity to the UAV flight path (e.g. 10 m ahead and behind) were monitored by visual observation.

3 | RESULTS

3.1 | Detection trial

1. The mean nest temperature at midday was 0.9°C (± SE 0.35) above ambient surface temperatures, which was significantly smaller than

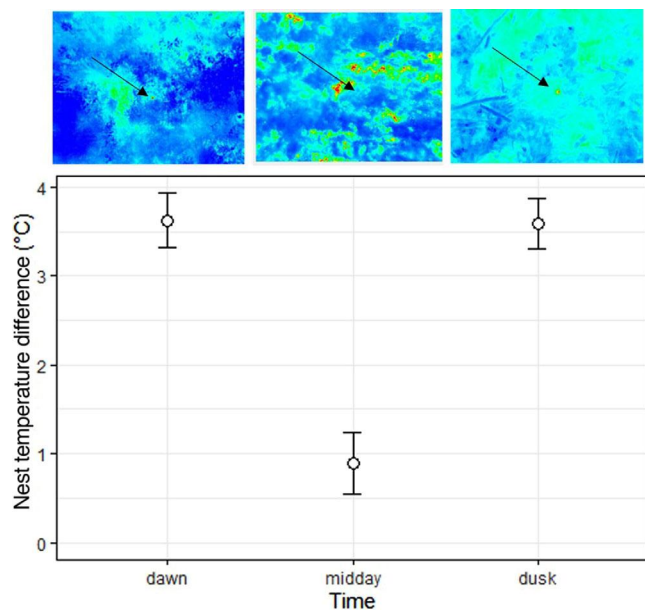**FIGURE 2** Resting posture of a nightjar on a nest (indicated by red outline)

FIGURE 3 Mean nest temperature differences (with standard errors) at dawn, midday and dusk (thermal images show nightjar nest 1 position at dawn, midday and dusk)

mean nest differences at dawn ($2.73 \pm$ SE 0.46, $t = 5.91$, $p < 0.0001$) and dusk ($2.69 \pm$ SE 0.45, $t = 6.00$, $p < 0.0001$, marginal $R^2 = 0.36$). This was reflected in the thermal imagery by nests being well-contrasted against the ground at both dusk and dawn, but very difficult to distinguish at midday (Figure 3). There was no significant difference in the mean nest temperature differences between dusk and dawn, nor were there any differences between nests or between nest stages (e.g. eggs or chicks).

2. Between 5 and 50 m flight altitudes, nightjar nest pixel counts ranged between 7 and 88 pixels. All nest locations were detectable from all utilized flight altitudes, although a minimum of around 20 pixels was required to distinguish the shape of the nightjar from other similar-sized warm objects. There was a linear relationship between flight altitude and nest pixel count between 5 and 30 m (Figure 4). Between 30 and 50 m, the pixel values varied between 6 and 10. Analysis conducted between 5 and 30 m revealed that each 1 m increase in flight altitude reduces the mean nest pixel count by 1.93 ± 0.26 pixels (marginal $R^2 = 0.51$, $df = 49$, $t = -7.266$, $p < 0.0001$). There were no significant differences in pixel counts between nests.

3.2 | Field trials

1. The survey identified two active nightjar nests (one attended by an adult male and two young fledglings (Nest 1); and one with an incubating female (Nest 2)) and four locations considered likely to be nightjar day roosts either with adult male presence or with evidence of nightjar occupation (e.g. lots of droppings; Figure 5). Of the 2607 images collected and analysed, 191 images contained hotspots that were highlighted for the ground verification survey. Many of the hotspots appearing in clusters were of the same warm objects appearing in multiple images (i.e. the position of the hotspot represents the location of the camera when it took the image). The ground surveys confirmed most of these hotspots as tree stumps, brash, and exposed surface rocks. The surveys also identified evidence of rabbits (e.g. mammal trails and droppings), and nests or roosts of smaller passerine species (e.g. meadow pipit (*Anthus pratensis*)).

3.3 | Disturbance monitoring

The attending birds were not observed responding to the presence of the UAV, even when it was as low as 5 m. Of the five nests observed at the Bryn study site, four were successful and one failed. This rate of success is consistent with the success rate of other monitored nests
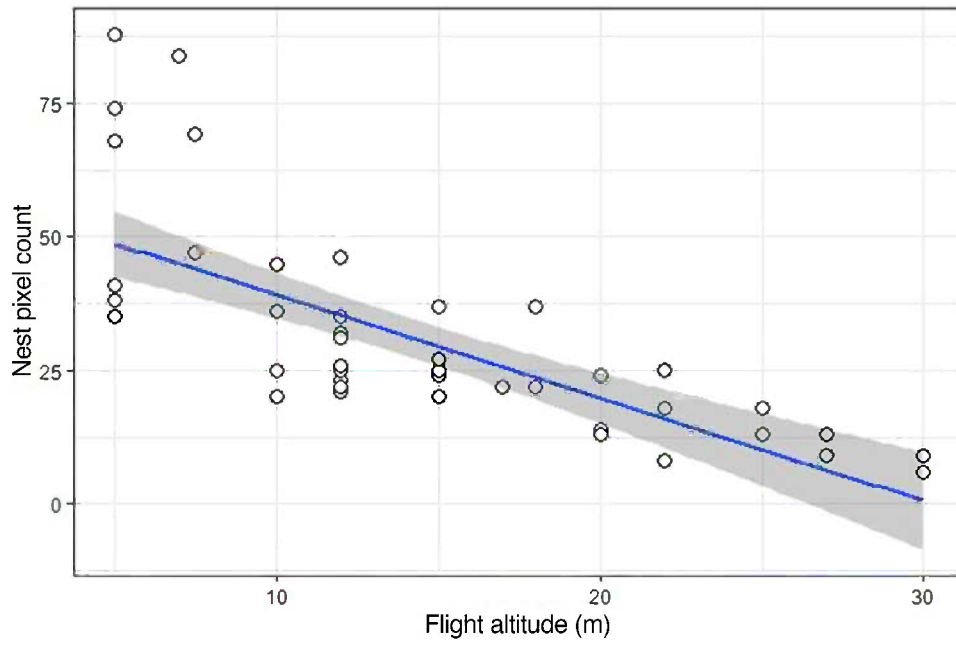
FIGURE 4 Nightjar nest pixel count by flight altitude (5–30 m only)
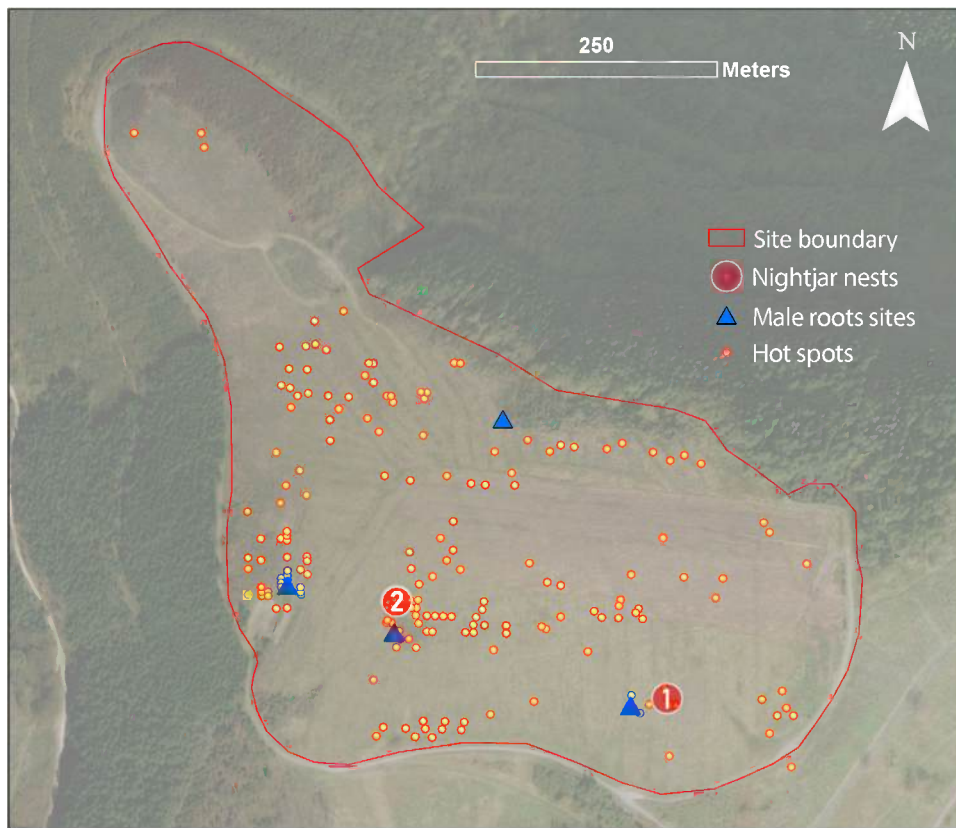

FIGURE 5 Post-analysis ground verification of hotspots at Cwmcarn

in Wales where no UAV survey work was completed (~60–70%; Personnel communication. Paddy Jenks, Tony Cross). There was limited observed response to the presence of the UAV by non-nightjar species. On one occasion during the field trial, a family of Ravens *Corvus corax* diverted from their flight line to perform a succession of aerial acrobatics (wing tucks, rolls and dives) within 25 m of the UAV. This behaviour lasted about 10 s before they left.

4 | DISCUSSION

4.1 | Findings

Nightjars are difficult to study because they are cryptic and nocturnal, and nests are difficult to find even if you are standing next to them (Troscianko et al., 2016). Traditional techniques for locating nests are time consuming, labour intensive, potentially disturbing to the birds and may be affected by an observer bias (Hodgson et al., 2018; Santangeli et al., 2020). This study confirms that UAV-mounted thermal cameras can locate cryptic ground-nesting birds over small to medium (~50 ha) survey areas. By relying on heat radiation, the influence of cryptic colouration and behaviour is removed. Thermal sensors mounted on UAVs offer a means of locating nests that in some contexts is more time efficient and may also be less disturbing, compared with visual-based methods. Also given the lack of significantly different thermal signatures between nests at different stages (e.g. egg or chick), perhaps because the adult represents both a good incubator of eggs and a good insulator of chicks, this approach is not influenced by the stage of nest development.

The study confirms that UAVs flown at dusk and dawn provide thermal imagery suitable for nest identification, although dawn also reduces the number of false positives from warm objects like rocks and tree stumps (Lethbridge et al., 2020; Santangeli et al., 2020). Increasing the time since sunset increases the thermal gradients of nests and reduces visual clutter from warm objects, but flying in darkness brings additional risks and reduces the visual line of sight between the operator and the UAV, which should be avoided (Stephenson et al., 2019). This contrasts with standard field survey methods for nightjar (Conway et al., 2007; Gilbert et al., 1998) that utilize dusk surveys based on known periods of activity. However, these survey methods are largely dependent on visual and acoustic cues and as such it is unsurprising this suggested timing is not optimal when reliant on thermal radiation.

Although this was not directly observed in this study, another important consideration is that dusk flights may coincide with adults leaving the nest or switching positions to embark on a foraging bout. This may make a dusk survey more likely to disturb the birds' natural behaviour, while dawn flights are more likely to encounter birds in a more settled status as the adults return to brood/ incubate the chicks or eggs at this time (Holyoak, 2001). Dawn surveys are in general suggested to be less disturbing than those at other times of day in a variety of bird and mammal species (Kays et al., 2019; Mulero-Pázmány et al., 2017; Witczuk et al., 2017).

Field trial flights identified two active nest sites in the Cwmcarn site confirming such a survey approach is capable of identifying nesting nightjars in areas with unknown presence, and no existing surveyor site knowledge that may bias results. The two nests are likely to be from the same female bird who, having raised one brood, initiated a second brood. The identification of two nests (one pair) within a 17-ha area is in line with known densities of breeding nightjar in similar habitats in Wales (0.38 and 0.82 males per km^2; Pritchard, 2021). This approach provided an approximate 50% surveying time reduction as full site coverage was possible in approximately 10 h of flight time versus a probable commitment in the order of 35 h to complete a through nest search of the Cwmcarn study area. It should be noted, however, that although this approach potentially provides a more rapid means of potential nest location across large areas, it is not a substitute for ornithological field expertise, which is required for narrowing down the area and interpreting observations in the field.

The high level of overlap (70%) of imagery in the field trial was incorporated to enable the generation of an orthorectified mosaic which 'stitches' the images together. In principle, this would reduce the clustering effect of multiple images containing the same warm object and enable automated classification of hotspots. This process was not possible for this dataset as the motion blur was too high to enable sufficient matching between images. Flying at lower speeds or in calmer conditions may improve the success of stitching.

4.2 | Recommendations

The study confirms that thermal surveys flown at dawn enhance the ability to differentiate between the nest and surrounding substrate using thermal imagery, as opposed to surveys at any other time. Thermal sensors have a low resolution compared to RGB sensors, which means that lower flight heights are required to detect medium-sized birds like nightjars (83 g, length 27 cm, wingspan: 60 cm; Robinson 2005). Low-level flights are more hazardous if there are tall trees and shrubs in the survey area, and if birds flush and attack the UAV. Lower flight heights also mean that flight time is longer per unit area, as this reduces the area of ground sampled by the camera in each image (increasing image resolution/decreasing pixel size), requiring more landing and battery replacements. The flight height trials revealed that, while increasing flight heights reduce the number of nest pixels per image, a flight height between 12 and 18 m provided similar mean results (Figure 4). These results should be considered with some caution, as the accuracy of object size estimates depends on the accuracy of the flight GPS and does not take into account terrain variation. This can be challenging in upland habitats because the terrain height is variable, and there are trees and shrubs in the transect that need to be avoided. The automated surveys fly at a fixed altitude from the take-off position so each transect needs to be roughly a similar topographical isoline. This may mean that a large number of false positives is unavoidable due to the margin of error in pixel size. This could be addressed through calibration of images with the integration of an

on-board LIDAR sensor, which can provide accurate flight height data, allowing more accurate hotspot scrutiny on the basis of size.

The classification of candidate nest sites utilized manual processing of images in the current study. However, it is possible to develop a machine-learning or artificial image professing protocol trained to recognize the heat signatures of a certain size (pixel cluster) and shape. This has been shown to be successful in the detection of thermal signatures of animals in previous UAV survey work and would be recommended for future applications (Lhoest et al., 2015; Longmore et al., 2017; Santangeli et al., 2020).

The requirement to have the visual line of sight between the nest and the thermal sensor to detect the heat of nests means that detection may be inhibited if the nest is beneath bracken or a fallen tree trunk; this can, however, be overcome through appropriate sensor orientation and flight overlap. To increase detection, we would recommend higher levels of transect overlap (e.g. this study used 70% overlap) with sensors pitched obliquely rather than objectively.

4.3 | Limitations

It should also be noted that as our study did not include a contrast with traditional survey methods we are unable to rule out the presence of false negatives and thus evaluate the relative approaches. Further research would be recommended to fully compare methods.

The use of UAV-mounted thermal detectors is also limited by the following factors:

1. The low resolution of thermal sensors requires low altitude flight in order to maximize detectability and pixel coverage.
2. Low flight elevation requires longer flight time per unit area and more consideration of the risk of collision with trees or posts.
3. Nest site identification is confounded by variable topography and the relative accuracy of UAV GPS location. This means that false positives are harder to exclude on the basis of size;

For the first two factors identified above, this is likely to mean the approach is most suitably deployed at relatively small targeted areas of interest (<100 ha) where risk is high (likely nests present) and works within the breeding season are required to accommodate other operational constraints. Further research and field trials are required to address factor three, with potential approaches using UAV mounted LIDAR in combination with an automated image processing technique.

5 | CONCLUSIONS

This study confirms that nesting and roosting nightjars can be detected using UAV-mounted thermal imaging and this when used in combination with verification survey is a highly promising method of nest location. It also confirms that this approach has potential to appropriately

inform upland land management decisions in a time-efficient manner where implemented by suitably experienced and qualified personnel (UAV licence required in addition to species-specific experience and knowledge).

AUTHORS' CONTRIBUTIONS

MS conceived the study. JV completed statistical analysis. MS and JV collected the data and jointly led the writing of the manuscript. Both authorscontributed critically to the drafts and gave final approval for publication.

ORCID

Jim O. Vafidis https://orcid.org/0000-0001-6013-4631

REFERENCES

Alexander, I., & Cresswell, B. (1990). Foraging by Nightjars *Caprimulgus europaeus* away from their nesting areas. *Ibis*, *132*(4), 568–574. https://doi.org/10.1111/j.1474-919X.1990.tb00280.x

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., & Green, P. (2015). Package "lme4" Version 1.1-12.

Bevan, E., Whiting, S., Tucker, T., Guinea, M., Raith, A., & Douglas, R. (2018). Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds. *PLoS One*, *13*(3), e0194460. https://doi.org/10.1371/journal.pone.0194460

Boonstra, R., Eadie, J., Krebs, C., & Boutin, S. (1995). Limitations of far infrared thermal imaging in locating birds. *Journal of Field Ornithology*, *1*, 192–198.

Boulton, R. L., & Cassey, P. (2012). How avian incubation behaviour influences egg surface temperatures: Relationships with egg position, development and clutch size. *Journal of Avian Biology*, *43*(4), 289–296. https://doi.org/10.1111/j.1600-048X.2012.05657.x

Bushaw, J. D., Ringelman, K. M., Johnson, M. K., Rohrer, T., & Rohwer, F. C. (2020). Applications of an unmanned aerial vehicle and thermal-imaging camera to study ducks nesting over water. *Journal of Field Ornithology*, *91*(4), 409–420. https://doi.org/10.1111/jofo.12346

Christie, K. S., Gilbert, S. L., Brown, C. L., Hatfield, M., & Hanson, L. (2016). Unmanned aircraft systems in wildlife research: Current and future applications of a transformative technology. *Frontiers in Ecology and the Environment*, *14*(5), 241–251. https://doi.org/10.1002/fee.1281

Cross, T., Lewis, J., Lloyd, J., Morgan, C., & Rees, D. (2005). *Science for conservation management: European Nightjar Caprimulgus europaeus breeding success and foraging behaviour in upland coniferous forests in mid-Wales*. Llandrindod Wells.

Conway, G., Wotton, S., Henderson, I., Langston, R., Drewitt, A., & Currie, F. (2007). Status and distribution of European Nightjars *Caprimulgus europaeus* in the UK in 2004. *Bird Study*, *54*(1), 98–111. https://doi.org/10.1080/00063650709461461

Couturier, T., Cheylan, M., Bertolero, A., Astruc, G., & Besnard, A. (2013). Estimating abundance and population trends when detection is low and highly variable: A comparison of three methods for the Hermann's

tortoise. *The Journal of Wildlife Management*, 77(3), 454–462. https://doi.org/10.1002/jwmg.499

Eaton, M. A., Aebischer, N. J., Brown, A., Hearn, R. D., Lock, L., Musgrove, A. J., Noble, D. G., Stroud, D. A., & Gregory, R. D. (2015). Birds of conservation concern 4: The population status of birds in the UK, Channel Islands and Isle of Man. *British Birds*, 108, 708–746

Esri inc. (2020) ArcGIS Desktop version 2.6, Redlands, CA: Environmental Systems Research Institute.

Galligan, E. W., Bakken, G. S., & Lima, S. L. (2003). Using a thermographic imager to find nests of grassland birds. *Wildlife Society Bulletin (1973–2006)*, 31(3), 865–869.

Gilbert, G., Gibbons, D. W., & Evans, J. (1998). *Bird monitoring methods: A manual of techniques for UK key species*. The Royal Society for the Protection of Birds, Sandy, Bedfordshire, UK.

Hodgson, J. C., Mott, R., Baylis, S. M., Pham, T. T., Wotherspoon, S., Kilpatrick, A. D., Raja Segaran, R., Reid, I., Terauds, A., & Koh, L. P. (2018). Drones count wildlife more accurately and precisely than humans. *Methods in Ecology and Evolution*, 9(5), 1160–1167. https://doi.org/10.1111/2041-210X.12974

Holyoak, D. T., & (2001). C. M. Perrins W. J. Bock & J. Kikkawa *Nightjars and their allies: The caprimulgiformes*. Bird Families of the World, Oxford University Press.

Israel, M., & Reinhard, A. (2017). Detecting nests of lapwing birds with the aid of a small unmanned aerial vehicle with thermal camera. In *2017 International Conference on Unmanned Aircraft Systems (ICUAS)* (pp. 1199–1207). IEEE.

Kays, R., Sheppard, J., Mclean, K., Welch, C., Paunescu, C., Wang, V., Kravit, G., & Crofoot, M. (2019). Hot monkey, cold reality: Surveying rainforest canopy mammals using drone-mounted thermal infrared sensors. *International Journal of Remote Sensing*, 40, (2), 407–419. https://doi.org/10.1080/01431161.2018.1523580

Langston, R., Liley, D., Murison, G., Woodfield, E., & Clarke, R. (2007). What effects do walkers and dogs have on the distribution and productivity of breeding European Nightjar *Caprimulgus europaeus*? *Ibis*, 149, 27–36. https://doi.org/10.1111/j.1474-919X.2007.00643.x

Lethbridge, M., Stead, M., & Wells, C. (2020). Estimating kangaroo density by aerial survey: A comparison of thermal cameras with human observers. *Wildlife Research*, 46(8), 639–648. https://doi.org/10.1071/WR18122

Liley, D., & Clarke, R. (2003). The impact of urban development and human disturbance on the numbers of nightjar *Caprimulgus europaeus* on heathlands in Dorset, England. *Biological Conservation*, 114, 219–230. https://doi.org/10.1016/S0006-3207(03)00042-9

Lhoest, S., Linchant, J., Quevauvillers, S., Vermeulen, C., & Lejeune, P. (2015). How many hippos (HOMHIP): Algorithm for automatic counts of animals with infra-red thermal imagery from UAV. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, 40, 6–13

Longmore, S. N., Collins, R. P., Pfeifer, S., Fox, S. E., Mulero-Pázmány, M., Bezombes, F., Goodwin, A., De Juan Ovelar, M., Knapen, J. H., & Wich, S. A. (2017). Adapting astronomical source detection software to help detect animals in thermal images obtained by unmanned aerial systems. *International Journal of Remote Sensing*, 38(8-10), 2623–2638. https://doi.org/10.1080/01431161.2017.1280639

Lowe, A., Rogers, A., & Durrant, K. (2014). Effect of human disturbance on long-term habitat use and breeding success of the European Nightjar, *Caprimulgus europaeus. Avian Conservation and Ecology*, 9, 6. https://doi.org/10.5751/ACE-00690-090206

McCafferty, D., Moncrieff, J., Taylor, I., & Boddie, G. (1998). The use of IR thermography to measure the radiative temperature and heat loss of a barn owl (*Tyto alba*). *Journal of Thermal Biology*, 23, 311–318. https://doi.org/10.1016/S0306-4565(98)00022-9

McEvoy, J. F., Hall, G. P., & McDonald, P. G. (2016). Evaluation of unmanned aerial vehicle shape, flight path and camera type for waterfowl surveys: Disturbance effects and species recognition. *PeerJ*, 4, e1831. https://doi.org/10.7717/peerj.1831

Mulero-Pázmány, M., Jenni-Eiermann, S., Strebel, N., Sattler, T., Negro, J. J., & Tablado, Z. (2017). Unmanned aircraft systems as a new source of disturbance for wildlife: A systematic review. *PloS One*, 12(6), e0178448. https://doi.org/10.1371/journal.pone.0178448

Murison, G. (2002). *The impact of human disturbance on the breeding success of the Nightjar Caprimulgus Europaeus on heathlands in South Dorset, England*. English Nature.

Pritchard, R. (2021) *Birds in Wales atlas*. Welsh Ornithological Society.

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rayner, J. (2016). *Behavioural and breeding ecology of a population of European nightjar Caprimulgus europaeus* (Doctoral dissertation), University of Nottingham.

Robinson, R. A. (2005). BirdFacts: Profiles of birds occurring in Britain & Ireland. BTO, Thetford. http://www.bto.org/birdfacts

Santangeli, A., Chen, Y., Kluen, E., Chirumamilla, R., Tiainen, J., & Loehr, J. (2020). Integrating drone-borne thermal imaging with artificial intelligence to locate bird nests on agricultural land. *Scientific Reports*, 10(1), 1–8. https://doi.org/10.1038/s41598-020-67898-3

Seymour, A., Dale, J., Hammill, M., Halpin, P., & Johnston, D. (2017). Automated detection and enumeration of marine wildlife using unmanned aircraft systems (UAS) and thermal imagery. *Scientific Reports*, 7, 1–10. https://doi.org/10.1038/srep45127

Shewring, M., & Carrington, D. (2015). European Nightjar–best practice mitigation measures during windfarm construction. In *Practice: Monitoring and Measuring Mitigation Success*, 19–23.

Shewring, M., & Vafidis, J. (2017). The effectiveness of deterrent measures to minimize disturbance impacts to breeding European nightjar at an upland wind farm site in South Wales, UK. *Conservation Evidence*, 14, 58–60.

Shewring, M., & Vafidis, J. (2021). Detecting the presence of nesting nightjar in upland clear-fell using drone-mounted thermal cameras, Dryad, Dataset, https://doi.org/10.5061/dryad.h70rxwdhq

Sparks, A. H., Hengl, T., & Nelson, A. (2017). GSODR: Global Summary Daily Weather Data in R. *Journal of Open Source Software*, 2(10), 177. https://doi.org/10.21105/joss.00177

Stephenson, M., Schulte, L., & Klaver, R. (2019). Quantifying thermal-imager effectiveness for detecting bird nests on farms. *Wildlife Society Bulletin*, 43, 302–307. https://doi.org/10.1002/wsb.962

Thomas, R. J., Lello, J., Medeiros, R., Pollard, A., Robinson, P., Seward, A., Smith, J., Vafidis, J., & Vaughan, I. (2017). Data analysis with R statistical software; A guidebook for scientists. Eco-Explore CIC. www.eco-explore.co.uk

Troscianko, J., Wilson-Aggarwal, J., Stevens, M., & Spottiswoode, C. N. (2016). Camouflage predicts survival in ground-nesting birds. *Scientific Reports*, 6, 19966. https://doi.org/10.1038/srep19966

Ward, R. J., Griffiths, R. A., Wilkinson, J. W., & Cornish, N. (2017). Optimising monitoring efforts for secretive snakes: A comparison of occupancy and N-mixture models for assessment of population status. *Scientific Reports*, 7(1), 1–12. https://doi.org/10.1038/s41598-017-18343-5

Weimerskirch, H., Prudor, A., & Schull, Q. (2018). Flights of drones over sub-Antarctic seabirds show species- and status-specific behavioural and physiological responses. *Polar Biol*, 41, 259. https://doi.org/10.1007/s00300-017-2187-z

Weston, M. A., O'Brien, C., Kostoglou, K. N., & Symonds, M. R. (2020). Escape responses of terrestrial and aquatic birds to drones: Towards a code of practice to minimize disturbance. *Journal of Applied Ecology*, 57(4), 777–785. https://doi.org/10.1111/1365-2664.13575

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., … Yutani, H. (2019). Welcome to

the tidyverse. *Journal of Open Source Software*, 4(43), 1686. https://doi.org/10.21105/joss.01686https://doi.org/10.21105/joss.01686

Witczuk, J., Pagacz, S., Zmarz, A., & Cypel, M. (2017). Exploring the feasibility of unmanned aerial vehicles and thermal imaging for ungulate surveys in forests – Preliminary results. *International Journal of Remote Sensing*, *39*(15–16), 5504–5521. https://doi.org/10.1080/01431161.2017.1390621

Witczuk, J., Pagacz, S., Zmarz, A., & Cypel, M. (2018). Exploring the feasibility of unmanned aerial vehicles and thermal imaging for ungulate surveys in forests-preliminary results. *International Journal of Remote Sensing*, *39*(15–16), 5504–5521.