

WILDLIFE BIOLOGY

Research article

Assessment of the accuracy of counting large ungulate species (red deer *Cervus elaphus*) with UAV-mounted thermal infrared cameras during night flights

Frank Zabel^{1,4}, Melanie A. Findlay² and Patrick J. C. White^{1,3}

¹School of Applied Sciences, Edinburgh Napier Univ., Edinburgh, UK

²Findlay Ecology Services, 2 Blakelaw Cottages, Kelso, UK

³Centre for Conservation & Restoration Science, Edinburgh Napier Univ., Edinburgh, UK

⁴Landesjagdverband Schleswig-Holstein e.V., Flintbek, Germany

Correspondence: Zabel Frank (40454942@live.napier.ac.uk)

Wildlife Biology

2023: e01071

doi: [10.1002/wlb3.01071](https://doi.org/10.1002/wlb3.01071)

Subject Editor:

Stephanie Kramer-Schadt

Editor-in-Chief: Ilse Storch

Accepted 17 January 2023



Unmanned aerial vehicles (UAVs) are increasingly used in wildlife surveying, including estimation of population densities. It is essential that we evaluate and test new survey methods to guide optimal sampling strategies. This study aimed to assess the accuracy of using a UAV-mounted thermal infrared (TIR) camera to count red deer *Cervus elaphus* populations, and how this was influenced by flight season, height and velocity, in order to help guide future census design. We flew 57 flights across a captive population of red deer in a 13 ha deer park enclosure of semi-natural habitat, representative of the species' range in northern Germany. Flights and image assessments were performed with no prior knowledge of actual population size. Accuracy was quantified by comparing real population size (known only to deer park staff) and independently estimated population sizes from UAV TIR images. Accuracy was significantly influenced by ecological season (early and late winter, spring and early summer) and height. Across all seasons, lower flights (100 m) performed better than higher ones (120 m), with lower flights in early winter and early summer being on average accurate to within 1% of actual population counts. For the season where we had the largest range of temperatures between flights (late winter) we found that accuracy was highest when temperatures were lowest. Flights were also able to identify all five stags (defined as a male deer ≥ 2 years old) present in early summer, but not in spring. Deer appeared to avoid the landing/take-off area, but there were no noted behavioural responses to drones flying over animals when at constant height and velocity during surveys. Our results indicate that UAV-mounted TIR camera have the potential to accurately count populations of large ungulate species, but that flight season, height and potentially temperature need to be taken into account to maximise accuracy. This approach has the potential to be scaled up to more accurately estimate densities of wild populations compared to existing approaches.

Keywords: drones, population census, population density, thermography, unmanned aerial vehicles (UAV)



www.wildlifebiology.org

© 2023 The Authors. Wildlife Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

One of the principal sources of data used by wildlife biologists and managers are population size or density estimates of species they are studying or managing in order to, among other things, monitor variation over time, assess impact of a potential management intervention or source of disturbance, or inform legal protection (Gregory et al. 2004). The optimal method and strategy require careful consideration of the target species and habitat, as well as sources of potential bias and logistical considerations (Sutherland 2006). Over time, in search of methods that are either more accurate, precise or logistically efficient, many biologists have sought to utilise new technologies for population monitoring, such as camera-traps (Foster and Harmsen 2012) and acoustic monitoring (Marques et al. 2013). The increasing array of 'off the shelf' digital technologies including sensor types and modes to deploy them is enabling research and monitoring to extend their reach to collect data in challenging environments and to new specifications (Arts et al. 2015). Unmanned aerial vehicles (UAVs), often also referred to as 'drones' can access difficult terrain and replace more traditional methods that are onerous and beset with logistical challenges, such as ground transects or boat surveillance. UAVs have facilitated a range of aerial surveys of species, often counting individuals (Adame et al. 2017, Edney and Wood 2021, Marchowski 2021) or other proxies of a population where counting of individuals is technically difficult, such as alligator nests (Elsey and Trosclair 2016) or complex aggregations of bird nests (Lyons et al. 2019).

Aerial surveys have many potential advantages over ground-based methods, a major one being that they give access to difficult terrain and allow approach to species that would be sensitive to approach by humans on foot (Chabot and Bird 2015). UAVs are frequently a safer, cheaper and more accessible method than using manned planes and helicopters (Witczuk et al. 2018). Reporting of general aerial surveys has significantly increased in peer-reviewed literature (Davis et al. 2022) including the use of UAVs as wildlife survey methods (reviewed by Robinson et al. 2022).

The more traditional aerial surveying approach of using human observers to count animals from planes and helicopters can be prone to undercounting (Cumberland 2012). Undercounting can be influenced by animal group size, light conditions, movement, size and colour of animals and vegetation density, while detectability is further affected by plane height and searching flight velocity (Jachmann 2002). Brack et al. (2018) introduced a framework for consideration of bias in abundance estimates from UAVs, recognising it may arise from four sources: 1) the 'availability' of an animal (i.e. is the animal available to be detected or is it completely concealed, for instance in a burrow), 2) the 'perception' of an animal (i.e. the animal may be 'available' but still has to be detected and identified correctly), 3) misidentification and 4) double counting. Overcounting is often not considered as a source of error, as it cannot readily be evaluated by most studies, yet it can be linked to misidentification of species (Davis et al. 2022).

The lack of on-board observers with UAVs necessitates sensor technology for data capture, such as red green blue (RGB) images, visible images or thermal infrared (TIR) imaging (Chrétien et al. 2015, Chabot and Francis 2016). Although UAVs are more accessible and safer than manned flights, they are still subject to potential detection bias (Brack et al. 2018). TIR imaging as an observation medium offers the ability to overcome the visual camouflage that can hide animals to standard surveillance, such as a light animal against a light background (Jachmann 2002). However, as with visible imagery, detection by TIR sensors from UAVs is also constrained by the 'availability' of animals, in that some individuals may be completely hidden by vegetation (Brack et al. 2018). To 'perceive' animals with TIR imagery, the observer must first detect an animal as an apparent warm spot compared with the background, and secondly the image must offer enough detail for the observer to identify the species and any other desired parameters, such as sex and age. TIR imagery itself can be affected by weather conditions, distance between the sensor and object, masking by vegetation, the physical properties of the animal's coat (which can compromise the animal's thermal footprint), and physical activity of the animal prior to survey (which can affect the heat dissipation and the animal's thermal footprint) (Cilulko et al. 2013). It is therefore important that the availability of animals is considered in UAV population studies, but also the perception of the target animals in context with the sensor type.

One of the pitfalls of assessing new methods for population estimates is that the number of individuals in the population of the study area is rarely known (Garner et al. 1995). Previous studies that have tried to assess the accuracy of UAV counting approaches have typically used comparisons with other survey methods, but ideally a true control is needed to know the absolute error rate of counts; in some cases, researchers have used dummy animals to assess accuracy (Hodgson et al. 2016) or compared manual and automated approaches to counting the same groups of animals (Marchowski 2021). Captive populations of known size in large enclosures provide an alternative approach to assess accuracy, but with the benefit that the animals may move and potentially behave as they would in the wild. For example, Rowcliffe et al. (2008) first tested the Random Encounter Model for estimation of population densities of unmarked mammals with camera traps within a large wildlife park, a method which has since been adopted and further tested in the wild (Manzo et al. 2012, Cusack et al. 2015).

Large ungulate species are often subject to human-wildlife conflicts (Carpio et al. 2021) and there is a need to foster their integrated management (van Beeck Calkoen et al. 2020). This necessitates reliable, accurate and user-friendly population count methods (Collier et al. 2007). For white-tailed deer *Odocoileus virginianus*, UAVs with TIR sensors have been shown to be more effective for census than spotlight surveys (Preston et al. 2021) and potentially accurate to within 10% of independent estimates made using ear-tags (Beaver et al. 2020), and this approach also has good potential for red deer *Cervus elaphus*. A feasibility study tested UAV

flights with TIR sensors for a group of mammals including red deer, finding that species identification across the range of target species could be difficult using the relatively low resolution TIR cameras, although red deer could be distinguished readily by their relatively large size (Witczuk et al. 2018). They found that other methodological challenges included the regulations limiting UAV use and weather conditions. Another recent study also tested antler detection with drone mounted TIR cameras, successfully identifying antlered deer at night during the antler growth period (Ito et al. 2022).

Given this potential for UAV-mounted TIR cameras to survey large ungulate species, the principle aim of this study was to assess whether the approach could deliver accurate population counts of a captive red deer population of known size. We also assessed which survey variables (survey season, height and velocity) would maximise accuracy and minimise any bias, ultimately in order to inform future survey protocols.

Material and methods

Study site

Our study site was the Wildpark Eekholt deer park in Germany (53.94869 N, 10.03051 E). This is located in the core of a surrounding red deer management area in the Segeberger Heide and closely emulates the habitat of the free roaming population. As well as red deer, the park also holds fallow deer *Dama dama*, sika deer *Cervus nippon* and wild boar *Sus scrofa*. We focussed on red deer both because they are the largest cervid species in central and western Europe and, with roe deer *Capriolus capriolus*, native to the surrounding area. Thus the method, if accurate, might be used in monitoring of wild populations. In addition, the 12.6 ha enclosure where two red deer compounds lie adjacent to each other, is the largest area of any species in the park, and thus emulated more closely the scale of monitoring in the wild. The layout allowed coverage of both compounds during one flight under the same technical and meteorological conditions. The flight area is bisected by the River Osterau with adjacent alluvial meadows and represents a mixed mosaic habitat, typical for the area. Approximately 40% of the area is covered by small patches of woodland, which are dominated by oak *Quercus* spp. and alder *Alnus glutinosa*.

Hardware and software used

The UAV was a tailormade UAV from the company Thermal Drones GmbH, Germany. The UAV was initially built and set up for fawn rescue. It has a maximum take-off weight of 2.5 kg and a payload of 0.15 kg. It has a diameter without propellers of 0.6 m and six propellers with a diameter of 0.25 m each. The UAV is powered by 16.4 V lithium polymer batteries with a power capacity of 130 Wh. The approximate flight time at 15°C is 18 min. The flight time decreases with lower temperatures and was approximately 12 min at 0°C.

The thermal images were taken by a Bosen thermal camera from FLIR, USA, with a focal length of 14.0 mm and 32° horizontal field-of-view, a sensor width of 7.68 mm, a height of 6.14 mm, an image size of 640W × 512H pixels. The images were recorded on a micro-SD card and manually transferred from the UAV to the analysis computer. Manual image analysis was performed with the software Poitagger, ver. 0.2.16, which has been developed at the Deutsches Zentrum für Luft- und Raumfahrt e.V. (the German Aerospace Center), Oberpfaffenhofen, Germany. We did not create an orthomosaic from the images because we decided this would risk duplication when deer moved during flights. Rather, we used the software to 'tag' each deer; tags were also then displayed on all other images which covered the location and it was therefore possible to estimate the new position of the deer in the other images and thus reduce the number of double counts.

Avoiding disturbance

To ensure that no animals were harmed by stress induced reactions, test flights were performed prior to this study, during which Deer Park employees observed the species within the study area as well as in the adjacent compounds. None of the animals were observed to react to the UAV nor showed any visible form of negative reaction during test flights. If animals had shown any signs of stress-related reactions during the test flights or during a later stage of the project, our contingency was to cease operations immediately and reassess the situation, but this did not occur. The take-off/landing site was selected to be 50 m outside of the fence for the red deer enclosure being surveyed.

Sampling design

To assess the suitability of using UAVs for the census of free ranging populations, it was key to find the right balance between detection accuracy and the size of the covered area. The latter is a function of flight altitude, flight velocity and side overlap (the overlap in images between two parallel flight transects). Having higher side overlap decreases the covered area per flight, but increases the likelihood to detect animals which are underneath trees or other vegetation, due to the overlapped areas being covered from two different angles (illustrated in Supporting information). As an optimal balance, we decided to set the front overlap between images at 75% and the side overlap at 50%.

Season affects red deer in two ways that could affect their 'availability' and also their 'perceptibility' (sensu Brack et al. 2018) during UAV censuses. Firstly, season affects how herds are organised. For most of the year, herds usually comprise single sex adults, with juveniles roaming with the female herds. However, during the rutting season in September, male herds disperse (Mitchell 1977) while female herds disperse in April, May or June, to give birth to their fawns (Mitchell 1977, Jaedrzejewski et al. 2006). Secondly, the morphology of deer changes through the seasons. In the study area, males

shed their antlers between January and March and immediately start to grow a new set of antlers (personal observations from local hunters and the corresponding author). Additionally, both sexes grow thick, insulative winter coats and are thought to reduce their metabolic activity during late winter (Arnold et al. 2004). Because we hypothesised that these seasonal differences in herding behaviour and morphology might influence detectability and the ability to gain demographic information, the method was tested in four seasons (early winter, late winter, spring and early summer), summarised in Table 1. We did not carry out surveys in mid or late summer when canopy cover and vegetation would be at their densest because we had an a priori assumption that both the availability and perceptibility (Brack et al. 2018) of deer to the TIR-mounted drones would be lower due to full or partial concealment by the tree canopy, and so resources were focussed on testing seasonal effects outside of this period.

In addition, we hypothesised that flight altitude and flight velocity would influence the accuracy of the method due to the interplay between flight velocity and height with aspects such as area surveyed, viewing angle and probability of double counting. Thus, during each season the factors flight altitude (m) and flight velocity (m s^{-1}) were included within a crossed treatment design with two levels of flight altitude (100 and 120 m) and three levels of flight velocity (8, 10, 12 m s^{-1}) making six treatments in total per season. Each treatment was replicated three times per season, whenever possible, making a maximum of 18 flights per season (and a maximum of 72 across the four seasons); this number of replicates was selected to balance accuracy of data and logistical constraints. Flights were repeated by cycling velocity within height within replicate. This ensured that if not all surveys were achievable (below) we would lose replicates but still have representations of each velocity-height combination.

Previous research has shown that tree cover significantly reduces the detectability of ungulates with RGB and thermal cameras (Franke et al. 2012). To increase detection probability,

the flights were therefore performed in the period between an hour after sunset and an hour before sunrise, when most free ranging red deer leave forested areas and move to the surrounding open areas to feed (Mattioli et al. 2022). Since flights were performed at night, an exemption from the night flight ban was applied for and granted by the Landesbetrieb Straßenbau und Verkehr Schleswig-Holstein, the responsible aeronautic authority. All UAV operations were performed by a trained and certified operator (the corresponding author) and in accordance with the rules and procedures outlined in the EU Regulations 2019/947 and 2019/945, which set the framework for the safe operation of UAVs in European skies (EU and EASA Member States).

Assessing accuracy of method for estimating population size

To assess the accuracy of the method, all flights were performed 'blind', i.e. with no prior knowledge of the actual size of the red deer population. This eliminated potential bias and replicated real world conditions where a surveyor would not know the population size. Staff at the deer park keep a stud book and thus know the number of deer in the enclosures at any one time, and how the number changes over time. Members of the deer park staff were asked to inform us of actual population sizes for each season flown (Table 1), but not send us those data until all images had been processed and our population size estimates made. All images were examined by the corresponding author to estimate the number of red deer and to report any observed sex and age specific features.

For each flight we then subtracted the actual number of deer (as provided by park staff) from those counted using the UAV, to calculate an absolute accuracy score, as follows:

$$\text{absolute accuracy} = \frac{\text{deer counted by UAV} - \text{known number of deer}}{\text{known number of deer}} \quad (1)$$

Table 1. Summary of four seasons surveyed for this study including weather conditions experienced during the study and the biological significance of selecting that season in the context of the red deer's annual cycle. 'Fawns' refer to young deer in their first year.

Season	Dates surveyed (2021)	Weather condition ranges during study				Deer characteristics		
		Humidity (%)	T°C	Fog	Tree canopy	Coat	Herding/fawns	Stags
Early winter	05/01	88–89	2	Absent	Bare	Winter coat	Large single-sex herds. Fawns not distinguishable.	All stags with antlers.
Late winter	18/03	90	0–6	Some	Bare	Winter coat	Large single-sex herds. Fawns not distinguishable.	All stags with antlers. Reduced metabolic activity (Arnold et al. 2004).
Spring	26/04 02/05	39–50 67–90	7–10 9–10	Absent Absent	Bare Bare	Beginning to moult out winter coat	Female herds split up to give birth to fawns. Males remain in single sex herds.	Antlers start growing on stags.
Early summer	21/06	78–81	15–17	Absent	Trees with leaves	Summer coat	Fawns distinguishable due to size.	Antler growth with high metabolic activity in stags (Li et al. 2014).

A negative number would indicate the UAV method had underestimated the population and a positive value that it had overestimated the population. We also converted these to relative accuracy scores by dividing the absolute accuracy score by the actual population size, as follows:

$$\text{relative accuracy} = \frac{\text{absolute accuracy}}{\text{known number of deer}} \quad (2)$$

We were thus able to quantify the extent of over/underestimation for different seasons, flight heights and flight velocities, replicated across multiple flights. We also attempted to do the same as above for stags (male deer ≥ 2 years old) and fawns, although low sample sizes of stags and lack of accurate deer park staff counts of fawns meant these data were not statistically analysed.

Treating absolute accuracy scores as a response variable, we used a generalised linear model with normal errors and identity link function to assess whether accuracy was related to any, or a combination, of the categorical variables season, flight height and flight velocity. Since we had a priori biological reasons to think season would be an important variable in detectability of deer to UAV-mounted TIR cameras (Table 1) we included season in all models. Unfortunately, because conditions did not allow every flight to be made, the intended sample size of 18 flights was lower in some seasons (12 in early winter, 16 in late winter and 11 in early summer). These reduced sample sizes of flights did not allow a full interaction model of season, flight height and flight velocity, nor an interaction model of season and flight velocity, since velocity was split into three levels. Thus, we tested a model containing season, flight height and their interaction (since flight height was only split into two levels) where flights of different velocities were pooled together. We used likelihood ratio tests with the Fisher–Snedecor-distribution (F-distribution) to first test for the significance of the interaction term and, if this was not significant, it was removed and we tested the significance of the main effects.

Since temperature is likely to play a role in the detectability of animals by TIR images, we also investigated the impact of ground temperature at time of flight on the absolute accuracy of our UAV-based red deer counts. At start of each flight, the temperature at the take-off/landing site was measured with a small digital thermometer. Temperatures, and degree of variation in temperatures, varied between flights and between seasons, having median values of 2°C (inter-quartile range (IQR) 2–2°C) in early winter, 3.5°C (IQR 0.8–5.3°C) in late winter, 9°C (IQR 9–10°C) in spring and 17°C (IQR 15–17°C) in summer. There was very little overlap between temperatures across seasons and thus temperature and season were largely confounded as variables. As such, we only assessed the effect of temperature on accuracy of flights separately within each season in turn, and then only for late winter, spring and early summer, since there was no variation in temperature for flights in early winter (2°C was recorded for each flight). Within each of those three seasons we tested a model with absolute accuracy as a response variable, and flight height,

ground temperature and the interaction between height and temperature. As above, we used likelihood ratio tests with the F-distribution to first test for the significance of the interaction term and, if this was not significant it was removed, and we tested the significance of the main effects.

The results of the likelihood ratio tests are presented with the Fisher–Snedecor value for the test (F) the degrees of freedom of the model being tested (which is the difference in the number of parameters being tested by the larger model and that of simplified version, e.g. with and without the interaction term) plus the residual degrees of freedom of the model (df). In addition, the p-value from an F-distribution with those numerator and denominator degrees of freedom was reported (p) and we used an α -level of $p < 0.05$ to indicate significance. Normality of model residuals were assessed visually using histograms. All analyses were performed in R Studio (R Studio Team 2020), using base R functions.

Results

A total of 24 642 images were captured during 72 flights and five flight nights (Table 1). Some flights had to be aborted mid-flight due to precipitation (rain and snow) which impairs lift and risks the drone stalling, so that the data from 57 flights were used in the analysis. No flights had to be cancelled or aborted due to strong winds.

Reaction of deer to UAV flights

During the survey period, the red deer appeared to avoid the proximity of the take-off/landing area during darkness, keeping a minimum distance of approximately 130 m from this area.

During main flight operations themselves (i.e. when the UAV was flying at a fixed velocity and height), no visible signs were observed that indicated that the UAV operation was negatively perceived by red deer within the flight area, nor by fallow deer or sika deer in adjacent compounds. The deer were not observed to seek any form of cover during UAV operation. For example, during early winter, a red deer herd rested for 93 min on a meadow. During this time six flights were performed yet very few deer changed their position (Fig. 1).

Accuracy of overall population counts

Visually, from UAV images, it was clear that season and/or meteorological conditions had an impact on perceptibility of red deer. For example, despite the late winter flight season being performed at temperatures between 0 and 6°C, the heat signatures of deer were indistinct and not well distinguishable from the surrounding vegetation, when compared to those taken in other seasons. For example, even at a similar temperature recorded at the take-off/landing site, deer were more distinctive in the images during flights in early winter compared to late winter (Fig. 2).

Our estimated counts of red deer based on UAV flights alone, when averaged across multiple flights at the same

height, ranged between 31.1 (at 120 m in late winter) and 49.6 (at 100 m in early summer) (Table 2a). In each season the estimated number of red deer was higher when flights were at 100 m than 120 m. Standard errors based on these estimates were never more than ± 1.6 deer (a coefficient of variation of 5.2%). The actual numbers of red deer in the enclosure, as revealed after the study by the deer park staff, ranged between 38 in late winter and spring, to 50 in early summer (Table 2a). For individual flights, independent UAV-based estimates ranged between an underestimate of 11 (30%) and an overestimate of 3 (6%). However, these values were significantly driven by season and flight height. There was no significant interaction between season and flight height ($F=0.84$, $df=3,49$, $p=0.478$), but when this interaction was removed, both season ($F=5.05$, $df=3,53$, $p=0.004$) and flight height ($F=9.43$, $df=1,52$, $p=0.004$) were significant. Averaging accuracy grouped by the two significant variables, season and flight height ($n=5-9$ per group), in most cases the approach underestimated the number of deer, with relative difference ranging between -17.3% and $+0.4\%$ (-7 and ± 0 deer in absolute terms) (Table 2a).

Flights at an altitude of 100 m were more accurate than those at 120 m across all four seasons, and late winter being the least accurate season for both altitudes (Table 2a). The accuracy per season and flight height for all red deer are shown in Fig. 3a.

In terms of the effect of temperature on absolute accuracy of drone flights, for late winter there was no significant interaction between flight height and temperature ($F=0.01$, $df=1,12$, $p=0.937$) but on removal of the interaction term, both height ($F=11.51$, $df=1,14$, $p=0.005$) and temperature ($F=15.46$, $df=1,13$, $p=0.002$) were significant. This model showed that in late winter temperature had a negative effect on absolute accuracy, and accuracy was generally higher at 100 m than 120 m height, such that accuracy was highest when temperatures were closer to 0°C and flights were at 100 m (Fig. 4).

For spring there was no significant interaction between flight height and temperature ($F=4.50$, $df=1,14$, $p=0.052$) and on removal of the interaction term, neither height ($F=0.44$, $df=1,16$, $p=0.517$) nor temperature ($F=3.86$,

$df=1,15$, $p=0.068$) were significant. Similarly for early summer, there was no significant interaction between flight height and temperature ($F=1.52$, $df=1,7$, $p=0.257$) and on removal of the interaction term, neither height ($F=1.64$, $df=1,9$, $p=0.236$) nor temperature ($F=3.21$, $df=1,8$, $p=0.111$) were significant. Finally, although we did not test an effect of temperature for early winter because it did not vary between flights, there was a significant effect of flight height on absolute accuracy ($F=6.66$; $df=1,10$; $p=0.027$), whereby mean absolute accuracy at 120 m (-2.8 deer) was significantly lower than at 100 m ($+0.2$ deer).

Accuracy of counts of adult males and juveniles

We chose to explore if it was possible to accurately count the number of stags (defined as adult males ≥ 2 years old) from drone-mounted TIR surveys. Following our surveys, the Deer Park indicated that there were five stags in the enclosure (Table 2b). During early and late winter it was not possible to distinguish between red deer sexes, so these were excluded from the stag analysis. In spring and early summer, it became possible to distinguish the sexes as the stags had already shed their old antlers and started to grow their new ones. As there were only five stags in the population no statistical analyses were undertaken, but our UAV-based estimates of the number of stags, taken as the mean per altitude per season ($n=5-9$ flights) varied widely in their accuracy, being as low as 2.4 (half missed on average) and as high as 5.0 (none missed in any flight) (Table 2b). Results appeared more accurate in early summer than spring for both altitudes, and for 100 m compared to 120 m for spring (Fig. 3b). The seasonal difference is likely a result of high metabolic activity in the almost fully grown antlers having a clearer heat signature to the TIR camera in early summer (Table 1).

During the early summer flight season, almost all red deer adult females had given birth to young. Fawns were frequently detected and correctly identified as such during our UAV flights, as they were mostly resting and could be identified by their relative size (Supporting information). One walking fawn was also identifiable despite its very small heat



Figure 1. Resting red deer between 20:20 and 21:53 h (93 min) on 5 January 2021, during which time six UAV flights were performed. There was very little discernible movement. Note the pictures were taken at different flight altitudes and velocities so the scale of the pictures is not comparable.

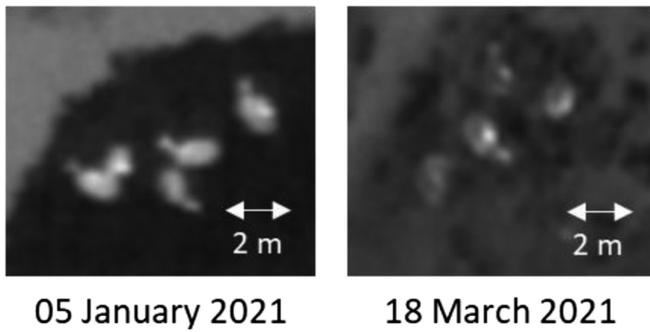


Figure 2. Thermal images of resting red deer taken during two seasons with different temperatures: left – 5 January 2021 (early winter) at 2°C; and right – 18 March 2021 (late winter) at 1°C. Both pictures were taken at a flight altitude of 100 m and a flight velocity of 10 m s⁻¹. Note temperatures were recorded at the take-off/landing site, not at the location of the drone or deer shown.

signature due to its close proximity to its mother (Supporting information). Due to the size and the structure of the compounds, the Deer Park staff could not accurately count the number of fawns, so we did not carry out a formal analysis of accuracy of drone-based estimates. However, across all flights, we underestimated fawn numbers relative to the estimates by Deer Park staff by 17%, with a minimum of 0% and a maximum of 33% per flight.

Discussion

Accuracy of method in an enclosed area

It is generally not possible to determine the accuracy of deer counting methods in the wild, as the actual number of deer

in free roaming populations is typically unknown (Daniels 2006), therefore, the decision was made to perform this study on a relatively large captive population (in semi-natural habitat) with a known number of deer. UAV flights and image analysis were performed with no prior knowledge of the population sizes, and our approach averaged a 2–3% underestimate of red deer in late winter, when thermal signatures of deer were poorest (Fig. 2), is excluded. As such UAV-mounted thermal cameras have been demonstrated to have potential to deliver accurate estimates of the size of a red deer population within a spatially defined area. In addition, although based on a low samples size of five animals, we demonstrated stags can be readily distinguished via this method if the survey flights are performed during the latter third of the antler growth, corresponding to our early summer flight season. We did not test our method during mid or late summer, focussing our resources on seasons when canopy cover was not dense, but future work might be able to assess the impact of canopy cover itself on accuracy of drone-based counts.

The method performed best at an altitude of 100 m in early winter (a 0.4% overestimate), spring (3.2% underestimate) and early summer (0.8% underestimate). In a study which used TIR camera-mounted drones to estimate density of captive white-tailed deer in Alabama, USA, estimated densities were, during evening flights (when the best contrast between animal and background were apparent), 8% lower than the mid-point of an independent abundance estimate made using ear-tagging of individual deer (Beaver et al. 2020). A study which used a manned microlight plane for the census of a captive red deer population within the wooded part of a 2.5 ha large compound, led, after five repetitions to underestimates of 15–22% (Franke et al. 2012), higher than those observed using UAV mounted TIR cameras in our study. Helicopters have also been deployed to count wild

Table 2. Comparison of actual and estimated (from UAV-mounted thermal imaging cameras) red deer counts in our captive study population for (a) all adult deer and (b) stags only. Data are grouped by season and flight height, but flights at different velocities (8, 10 and 12 m s⁻¹) have been pooled because sample sizes did not allow us to model the effect of velocity.

Season	Height (m)	Number of flights (n)	Mean estimates of red deer numbers across all flights for that altitude and season	SE	Actual number of red deer (n)	Mean absolute accuracy	Mean relative accuracy	Coefficient of variation for mean values (CV)
(a) All adult deer								
Early winter	100	6	44.17	± 0.78	44	+0.17	+0.39%	1.8%
	120	6	41.33	± 1.10	44	-2.67	-6.07%	2.7%
Late winter	100	9	35.00	± 1.07	38	-3.00	-7.89%	3.1%
	120	7	31.14	± 1.62	38	-6.57	-17.29%	5.2%
Spring	100	9	36.78	± 1.03	38	-1.22	-3.21%	2.8%
	120	9	35.89	± 1.46	38	-2.11	-5.55%	4.1%
Early summer	100	5	49.60	± 1.14	50	-0.40	-0.8%	2.3%
	120	6	47.83	± 1.54	50	-2.17	-4.34%	3.2%
(b) Stags								
Spring	100	9	3.67	± 0.49	5	-1.33	-27%	13.4%
	120	9	2.44	± 0.69	5	-2.56	-51%	28.3%
Early summer	100	5	5.00	± 0.14	5	0.00	0%	2.8%
	120	6	4.83	± 0.18	5	0.17	-3%	3.7%

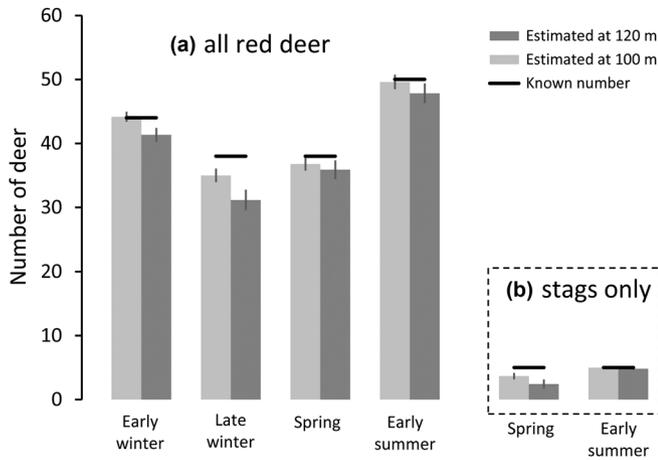


Figure 3. Estimates of captive population of (a) all red deer and (b) red deer stags only (males ≥ 2 years old), at a deer park from thermal images taken from drone flights at two flight heights (100 m, 120 m) in four seasons, compared to known numbers. Note that stags were not identifiable from drones in early and late winter so are excluded (main text). Error bars are standard errors based on replicate flights (Table 2). ‘Known numbers’ refer to count of deer known by deer park staff and only provided to the authors at the data analysis stage, thus flights were conducted with no prior knowledge of these counts.

red deer, these flights are often performed at very low flight altitudes, of 40–50 m (Freddy et al. 2004). This study was performed in the wild on an unknown population size, so it not possible to compare the accuracy with our method.

Manned-flight operations are risky for the people and the equipment involved, they may be highly intrusive and potentially pose significant psychological and physical stress to the surveyed animals and other species in the area (Bates et al. 2021). The UAV approach tested in this study appears to deliver accurate results while being also less risky for the operators, less cost intensive and more flexible than deer

counts via microlight planes and helicopters. In addition, our UAV operation appeared not to pose any stress to the animals, although we did not take any measures of physiological responses. Drones may also reduce disturbance by minimising the need for ground-based survey approaches where close approach by surveyors may needed to obtain accurate counts (for example in waterbird flocks: Marchowski 2021).

As well as accuracy, consistency within a sampling approach is important. The coefficients of variation (CV, a measure of between-flight consistency in count) of our UAV method, for the flights performed at an altitude of 100 m, were low, at 1.8% in early winter, 2.8% in spring and 2.3% in early summer. Other methods with a similarly low risk profile and level of intrusiveness can have much wider ranges of variation. For example, a comparison of three survey methods performed on a roe deer population in Italy, found a CV of 58% for drive counts, 27% for a random encounter method and 12% for pellet group counts (Marcon et al. 2019).

For late winter only, we found a significant effect of temperature (recorded at the take-off site) on accuracy of counts, whereby lower temperatures produced more accurate (i.e. less underestimated) estimates of deer numbers, across a range of 0°C and 6°C. The lack of a temperature effect on accuracy in other seasons may just reflect the low variation in temperatures recorded, and so further investigation outside the winter season would be useful. We would expect that temperature should influence thermal imaging for surveying animals, since it relies on a contrast between a target animal’s temperature and the background. Indeed, thermal imaging of Eurasian otters *Lutra lutra* on land has shown that the relationship between the temperature of their coat (which can vary widely due to immersion in water) and the background can heavily influence their thermal signature (Kuhn and Meyer 2009) which in turn can influence their detection probability to passive-infra red detectors (Findlay et al. 2020). Beaver et al. (2020) found accuracy of TIR camera-mounted drones highest when surveying in the evening compared to morning, due

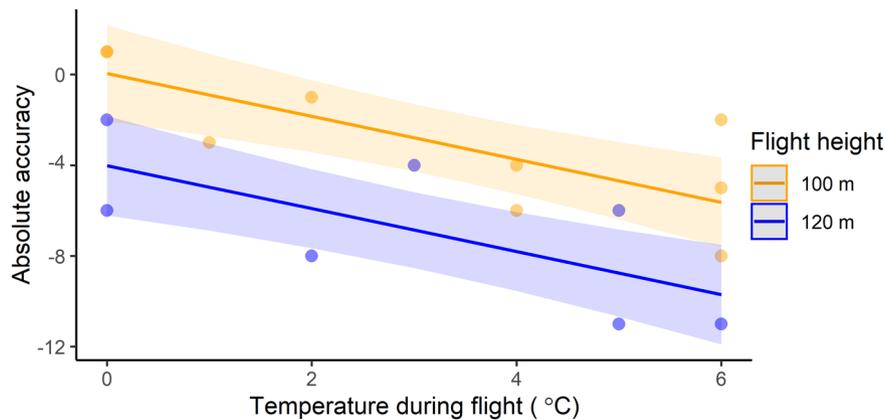


Figure 4. Modelled relationship between absolute accuracy of drone flights (the difference between the true population of red deer and those estimated from flights), where a value of zero represents perfect accuracy, positive values overestimates and negative values underestimates), flight height (100 m or 120 m) and ground temperature at take-off (range 0–6°C) during the late winter survey. Each flight is represented by a point. Lines are from a generalised linear model with normal errors and identity link function (text) and shaded areas represent 95% confidence regions.

to better thermal contrast between animals and background. We did not record ground or air temperatures specifically, so it is difficult to elucidate the exact mechanisms involved, but it may be that our accuracy was highest at lower recorded temperatures due to a lower ground surface/vegetation temperature and thus higher thermal contrast of the red deer.

This study has shown that the deer census by UAV-mounted thermal cameras can potentially offer a viable alternative to alternative ground-based or manned-flight methods and that it can provide more accurate and highly detailed data about the ungulate communities within the census area. The method has a high potential for the application within wildlife management and conservation and to be scaled up for free roaming populations of red deer and other species, but there are several considerations to make and obstacles to overcome.

Scaling up to wild populations: opportunities, limitations and knowledge gaps

Our study demonstrates that the accuracy of censusing deer using UAV-mounted TIR cameras may be influenced by morphology and differences in the metabolic activity of the deer in context of the season, as well as survey specifications (e.g. flight altitude). It is likely that these impact aspects of availability and perceptibility of deer to the surveys (Brack et al. 2018). The influence of these factors may vary with species and habitat structure and so are likely to need to be determined for different species surveyed, and in different geographical areas, on a case-by-case basis. Our approach of assessing accuracy against a population of known size within a captive environment provides a framework for assessing and optimising the approach for a specific context and survey goal, although this may depend on the size of the captive population and the habitat in the enclosure. In our case the enclosure contained habitat similar to the surrounding area and was thus considered representative.

In the wild, study populations may be spread over a much larger area and at lower densities than in our study enclosures (deer in our study were at densities of between 3 and 4 per hectare). As such, censusing may not always be an option, and rather managers or ecologists may wish to sample across a wider area (perhaps using a stratified random sampling approach to account for habitat differences) and extrapolate a density estimate from that (Gregory et al. 2004). The spatiotemporal sampling distribution would need to be carefully planned to ensure a representative sample of flight areas, although our observations suggest the take-off/landing areas for each should be carefully chosen to be at some distance to the survey area. We did not directly test the accuracy of a sampling-based approach, but our results may inform elements of such an approach, by indicating optimal times of year and flight height at which to perform them, or else provide a framework to assess that for specific species or geographic areas.

Our results for red deer suggest that the optimal time for surveying is likely to be early winter or early summer, with

the latter having the benefit that stags are more readily identifiable (Table 2a), which may provide data on sex ratio. Fawns were also identifiable at that time of year which may give an index of breeding success, although we were not able to assess accuracy of fawn counts in full. Our results also indicate that a lower altitude of 100 m gave more accurate results, although in some seasons altitude was not a significant factor. Indeed, the seasons when a lower altitude was more accurate (early and late winter) had the worst weather conditions and included a period (late winter) when metabolic activity is reduced (Arnold et al. 2004), so the lower altitude likely compensated for these limitations, reducing number of undetected deer and thus study bias. Other UAV surveys have used lower flight altitudes, but our view is that flights lower than 100 m would substantially decrease surveyed area per flight, whilst potentially increasing risk of disturbance to animals.

Weather in general is a critical factor in UAV operations. During our field work weather conditions often changed rapidly and unexpectedly, reducing the number flights we could carry out from 72 to 57 (a 21% reduction). This is an issue which affects almost all deer counting methods, such as spotlight counts (Garel et al. 2010) and counts from planes and helicopters (Franke et al. 2012) and must be factored in to resourcing of surveys. Equipment and human resources should be secured with sufficient buffer times and preferably also at different time slots, to allow for adverse weather. Assessing the direct impact of weather conditions on accuracy, while avoiding confounding effects of season, would have required us to survey across multiple nights per season with varying weather conditions, which we logistically could not do, but this may be an avenue for future research.

Double counting creates a potential source of bias in drone surveys (Brack et al. 2018) but this is unlikely to have been a source of bias in this study, since it would tend to lead to overestimates of populations, not underestimates as we consistently observed. In addition, double counting might be expected to be higher in species that move more rapidly around the landscape (including predatory species roaming for prey), rather than herbivores. Nevertheless, this would require consideration when scaling up to wild populations. One source of double counts is when deer are captured twice, once while the UAV flies over a certain area and again, when the UAV returns on a parallel route to image the bordering area. This bias could potentially be reduced by decreasing the number of intersection lines between the different areas by using multiple drones flying in parallel, although such a technique would have high logistical demands and would require rigorous testing.

A further potential source of bias is habitat structure. Tree cover may make animals harder to detect by thermal imaging. This can be partially countered by the side overlap of the images taken, the overlap between two flight transects (Supporting information), which in our study was set to 50%. This has the effect that if an animal is below a tree canopy, it is more likely to be captured because it may be taken from different angles, one of which may reveal a clearer image than others. Overlap decreases the area a given UAV can cover in

a given flight, but we suggest it should not be sacrificed to cover a larger area, because that may reduce accuracy.

Species identification was not a main aspect of this study because species were separated by enclosures and the UAV operator and image analyser knew the enclosure each image represented. Species identification would be very important when using UAV surveys for wild populations either to eliminate non target animals or, in a multi-species survey, to correctly label individuals. Species misidentification is also considered an important source of bias in UAV studies (Brack et al. 2018). Species identification may be more challenging when using TIR images, in which colouration cannot be used as an identification feature, unlike with RGB images. Potentially, day-time flights could be performed to obtain complementary RGB images, although in some species cover may be sought during the daytime so the same animals may be hidden. There are some ways species identification accuracy could be improved with TIR images. If there are no obvious features, like growing antlers, which simplify the species identification, the size of the biggest animals within a group could potentially be used as an indicator for the species of that group. Given that the resolution at ground level (in e.g. cm per pixel) is a function of the camera resolution, camera angle and the flight height, then the actual body length of pictured animals might be estimated by multiplying the ground resolution with an animals estimated body length in pixels.

Conclusions

We have demonstrated that UAV-based thermal imaging surveys can offer a non-invasive but potentially very accurate and precise surveying approach to estimate red deer population numbers, sex-ratios and possibly breeding success. Specifically for red deer in northern Europe, for the most accurate total population counts we would recommend flights at 100 m, rather than 120 m, in early winter or early summer. For the most accurate counts of stags, we would recommend flights in early summer, corresponding to when vegetation growth is still reduced and antler growth is developed. We were not able to assess the effect of flight velocity on accuracy, so future research is required to investigate that aspect of flight protocols. These results may be specific to red deer in northern Europe, but our study provides a framework to test this approach in other geographical areas/biomes and for other species. The application to larger, free-ranging populations needs testing, and wildlife managers would need to consider aspects such as sampling design, species identification, double counting and cost implications when doing so.

Acknowledgements – A special thanks to the Wildpark Eekholt for the permission to conduct the project within their park and for providing the population data. Many thanks also to Wildtierrettung Segeberger Heide e.V. for providing the drone system for the study and also a great thank you to Tobias Dahms, Moritz Franz-Gerstein,

Dr Oliver Keuling and Walter Mahnert for their help with the species identification. Thanks to four anonymous reviewers for helpful comments on an earlier draft.

Funding – No external funding has been received for the execution of this project.

Author contributions

Zabel Frank: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Project administration (lead); Resources (equal); Software (equal); Supervision (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Mel Findlay:** Formal analysis (equal); Investigation (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Patrick White:** Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1002/wlb3.01071>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://datadryad.org/stash/share/jveB0kwhpwCVufAGmFNkhGTXLjDtOpltcxwGVSI2Chg> (Frank et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Adame, K., Pardo, M. A., Salvadeo, C., Beier, E. and Elorriaga-Verplancken, F. R. 2017. Detectability and categorization of California sea lions using an unmanned aerial vehicle. – *Mar. Mamm. Sci.* 33: 913–925.
- Arnold, W., Ruf, T., Reimoser, S., Tataruch, F., Ondersheka, K. and Schober, F. 2004. Nocturnal hypometabolism as an overwintering strategy of red deer *Cervus elaphus*. – *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 286: 174–181.
- Arts, K., van der Wal, R. and Adams, W. M. 2015. Digital technology and the conservation of nature. – *Ambio* 44: 661–673.
- Bates, S. B., Whiting, J. C. and Larsen, R. T. 2021. Comparison of effects of shed antler hunting and helicopter surveys on ungulate movements and space use. – *J. Wildl. Manage.* 85: 437–448.
- Beaver, J. T., Baldwin, R. W., Messinger, M., Newbolt, C. H., Ditchkoff, S. S. and Silman, M. R. 2020. Evaluating the use of drones equipped with thermal sensors as an effective method for estimating wildlife. – *Wildl. Soc. Bull.* 44: 434–443.

- Brack, I. V., Kindel, A. and Oliveira, L. F. B. 2018. Detection errors in wildlife abundance estimates from unmanned aerial systems (UAS) surveys: synthesis, solutions and challenges. – *Methods Ecol. Evol.* 9: 1864–1873.
- Carpio, A. J., Apollonio, M. and Acevedo, P. 2021. Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. – *Mamm. Rev.* 51: 95–108.
- Chabot, D. and Bird, D. M. 2015. Wildlife research and management methods in the 21st century: where do unmanned aircraft fit in? – *J. Unmanned Veh. Syst.* 3: 137–155.
- Chabot, D. and Francis, C. M. 2016. Computer-automated bird detection and counts in high-resolution aerial images: a review. – *J. Field Ornithol.* 87: 343–359.
- Chrétien, L., Théau, J. and Menard, P. 2015. Wildlife multispecies remote sensing using visible and thermal infrared imagery acquired from an unmanned aerial vehicle (UAV), Vol. 40. – *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences – ISPRS Archives*, pp. 241–248.
- Cilulko, J., Janiszewski, P., Bogdaszewski, M. and Szygielska, E. 2013. Infrared thermal imaging in studies of wild animals. – *Eur. J. Wildl. Res.* 59: 17–23.
- Collier, B. A., Ditchkoff, S. S., Raglin, J. B. and Smith, J. M. 2007. Detection probability and sources of variation in white-tailed deer spotlight surveys. – *J. Wildl. Manage.* 71: 277–281.
- Cumberland, R. E. 2012. Porvin double-count aerial surveys in New Brunswick: are results reliable for moose? – *ALCES* 48: 66–77.
- Cusack, J. J., Swanson, A., Coulson, T., Packer, C., Carbone, C., Dickman, A. J., Kosmala, M., Lintott, C. and Rowcliffe, J. M. 2015. Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. – *J. Wildl. Manage.* 79: 1014–1021.
- Daniels, M. J. 2006. Estimating red deer *Cervus elaphus* populations: an analysis of variation and cost-effectiveness of counting methods. – *Mamm. Rev.* 36: 235–247.
- Davis, K. L., Silverman, E. D., Sussman, A. L., Wilson, R. R. and Zipkin, E. F. 2022. Errors in aerial survey count data: Identifying pitfalls and solutions. – *Ecol. Evol.* 12: 1–14.
- Edney, A. J. and Wood, M. J. 2021. Applications of digital imaging and analysis in seabird monitoring and research. – *Ibis* 163: 317–337.
- Else, R. M. and Trosclair, P. L. 2016. The use of an unmanned aerial vehicle to locate alligator nests. – *Southeast. Nat.* 15: 76–82.
- Findlay, M. A., Briers, R. A. and White, P. J. C. 2020. Component processes of detection probability in camera-trap studies: understanding the occurrence of false-negatives. – *Mamm. Res.* 65: 167–180.
- Foster, R. J. and Harmsen, B. J. 2012. A critique of density estimation from camera-trap data. – *J. Wildl. Manage.* 76: 224–236.
- Frank, Z., Findlay, M. A. and White, P. J. C. 2023. Data from: Assessment of the accuracy of counting large ungulate species (red deer *Cervus elaphus*) with UAV-mounted thermal infrared cameras during night flights. – Dryad Digital Repository, <https://datadryad.org/stash/share/jveB0kwhpwCVufAGm-FNkhGTXLjDtOpltcxwGVS12Chg>.
- Franko, U., Goll, B., Hohmann, U. and Heurich, M. 2012. Aerial ungulate surveys with a combination of infrared and high-resolution natural colour images. – *Anim. Biodivers. Conserv.* 35: 285–293.
- Freddy, D. J., White, G. C., Kneeland, M. C., Kahn, R. H., Unsworth, J. W., deVergie, W. J., Graham, V. K., Ellenberger, J. H. and Wagner, C. H. 2004. How many mule deer are there? Challenges of credibility in Colorado. – *Wildl. Soc. Bull.* 32: 916–927.
- Garel, M., Bonenfant, C., Hamann, J. L., Klein, F. and Gaillard, J. M. 2010. Are abundance indices derived from spotlight counts reliable to monitor red deer *Cervus elaphus* populations? – *Wildl. Biol.* 16: 77–84.
- Garner, D. L., Underwood, H. and Porter, W. 1995. Use of modern infrared thermography for wildlife population surveys. – *Environ. Manage.* 19: 233–238.
- Gregory, R. D., Gibbons, D. W. and Donald, P. W. 2004. Bird census and survey techniques. – In: Sutherland, W. J., Newton, I. and Green, R. E. (eds), *Bird ecology and conservation: a handbook of techniques*. Oxford Univ. Press, pp. 17–55.
- Hodgson, J. C., Baylis, S. M., Mott, R., Herrod, A. and Clarke, R. H. 2016. Precision wildlife monitoring using unmanned aerial vehicles. – *Sci. Rep.* 6: 1–7.
- Ito, T. Y., Miyazaki, A., Koyama, L. A., Kamada, K. and Nagamatsu, D. 2022. Antler detection from the sky: deer sex ratio monitoring using drone-mounted thermal infrared sensors. – *Wildl. Biol.* 2022: 4.
- Jachmann, H. 2002. Comparison of aerial counts with ground counts for large African herbivores. – *J. Appl. Ecol.* 39: 841–852.
- Jaedrzejewski, W., Spaedtke, H., Kamler, J. F., Jaedrzejewska, B. and Stenkewitz, U. 2006. Group size dynamics of red deer in Białowieża Primeval Forest, Poland. – *J. Wildl. Manage.* 70: 1054–1059.
- Kuhn, R. A. and Meyer, W. 2009. Infrared thermography of the body surface in the Eurasian otter *Lutra lutra* and the giant otter *Pteronura brasiliensis*. – *Aquat. Biol.* 6: 143–152.
- Li, C., Zhao, H., Liu, Z. and McMahon, C. 2014. Deer antler - A novel model for studying organ regeneration in mammals. – *Int. J. Biochem. Cell Biol.* 56: 111–122. <https://doi.org/10.1016/j.biocel.2014.07.007>.
- Lyons, M. B., Brandis, K. J., Murray, N. J., Wilshire, J. H., McCann, J. A., Kingsford, R. T. and Callaghan, C. T. 2019. Monitoring large and complex wildlife aggregations with drones. – *Methods Ecol. Evol.* 10: 1024–1035.
- Manzo, E., Bartolommei, P., Rowcliffe, M. J. and Cozzolino, R. 2012. Estimation of population density of European pine marten in central Italy using camera trapping. – *Acta Theriol.* 57: 165–172.
- Marchowski, D. 2021. Drones, automatic counting tools and artificial neural networks in wildlife population censusing. – *Ecol. Evol.* 11: 16214–16227.
- Marcon, A., Battocchio, D., Apollonio, M. and Grignolio, S. 2019. Assessing precision and requirements of three methods to estimate roe deer density. – *PLoS One* 14: e0222349.
- Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Moretti, D. J., Harris, D. and Tyack, P. L. 2013. Estimating animal population density using passive acoustics. – *Biol. Rev.* 88: 287–309.
- Mattioli, S., Zachos, F., Rossi, L., Lister, A. and Corlatti, L. 2022. Red deer *Cervus elaphus* Linnaeus, 1758. – In: Hackländer, H. and Zachos, F. (eds), *Handbook of the mammals of Europe*. Springer Nature, pp. 1–37.
- Mitchell, B., Staines, B. W. and Welch, D. 1977. Ecology of red deer: a research review relevant to their management in Scotland. – *Inst. of Terrestrial Ecology*.
- Preston, T. M., Wildhaber, M. L., Green, N. S., Albers, J. L. and Debenedetto, G. P. 2021. Enumerating white-tailed deer using unmanned aerial vehicles. – *Wildl. Soc. Bull.* 45: 97–108.
- R Studio Team 2020. RStudio: integrated development – <https://posit.co/downloads/>.

- Robinson, J. M., Harrison, P. A., Mavoja, S. and Breed, M. F. 2022. Existing and emerging uses of drones in restoration ecology. – *Methods Ecol. Evol.* 13: 1899–1911.
- Rowcliffe, J. M., Field, J., Turvey, S. T. and Carbone, C. 2008. Estimating animal density using camera traps without the need for individual recognition. – *J. Appl. Ecol.* 45: 1228–1236.
- Sutherland, W. J. 2006. *Ecological census techniques: a handbook*. – Cambridge Univ. Press.
- van Beeck Calkoen, S. T. S., Mühlbauer, L., Andrén, H., Apollonio, M., Balčiauskas, L., Belotti, E., Carranza, J., Cottam, J., Filli, F., Gatiso, T. T., Hetherington, D., Karamanlidis, A. A., Krofel, M., Kuehl, H. S., Linnell, J. D. C., Müller, J., Ozolins, J., Premier, J., Ranc, N., Schmidt, K., Zlatanova, D., Bachmann, M., Fonseca, C., Lonescu, O., Nyman, M., Šprem, N., Sunde, P., Tannik, M. and Heurich, M. 2020. Ungulate management in European national parks: why a more integrated European policy is needed. – *J. Environ. Manage.* 260: 110068.
- Witczuk, J., Pagacz, S., Zmarz, A. and Cypel, M. 2018. Exploring the feasibility of unmanned aerial vehicles and thermal imaging for ungulate surveys in forests – preliminary results. – *Int. J. Remote Sens.* 39: 5504–5521.