

RESEARCH ARTICLE

Efficient data collection for camera trap-based density estimation: A preliminary assessment

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Abstract

1. Camera traps have great potential for generating wildlife insights by providing high resolution site-specific data. Methods of data collection and analysis reliant on these tools for population density estimation can be relatively resource intensive, hindering their mainstream adoption.
2. Here, we explore the potential of population density estimates derived from a distance sampling method based on optics theory, which greatly simplifies the process of setting up camera sites and analysing data. Specifically, we (1) tested the method on human subjects in an artificial environment, (2) compared it to another method relying on virtual grids on images using wild populations of black-backed jackal (*Canis mesomelas*) and African civet (*Civettictis civetta*) in South Africa and (3) deployed it to estimate wild boar (*Sus scrofa*) population densities in Hungary.
3. The initial human trials resulted in an estimate that was extremely close to true population density. When compared to the virtual grid method, results suggest that our distance sampling method can deliver accurate estimates with increased convenience and robustness against disruptions of the camera sites. The wild boar study resulted in a realistic density estimate, which can be used as a baseline when assessing future fluctuations in population density.
4. As this new approach does not have special requirements for setting up camera sites, it is efficient and widely applicable across other density estimation methods requiring an estimate for effective detection distance. Additionally, the method can be applied in the retrospective analysis of existing datasets.

KEYWORDS

camera trapping, distance sampling, ecological monitoring, population density estimation, remote sensing, wildlife management

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1 | INTRODUCTION

With the rate of species loss currently at an all-time high (Cardinale et al., 2012), monitoring remaining populations is more important than ever to inform and assess the efficiency of conservation policies. The use of density indices was formerly considered to be sufficient to monitor the effects of most ecological problems (Caughley, 1977), but it is increasingly apparent that the success of management decisions largely depends on the accuracy of measurements (Nichols & Williams, 2006). Accurate density surveys are typically resource-intensive, creating a strong incentive to develop more efficient methods that maintain accuracy.

The last 15 years have seen rapid developments in using camera traps to monitor the abundance and population density of species that cannot be individually identified. Recently proposed methods include relative abundance indices (Kuprewicz, 2013; O'Brien, 2011), occupancy models (MacKenzie & Royle, 2005), the random encounter model (REM; Rowcliffe et al., 2008) and its variations, random encounter and staying time (REST; Nakashima et al., 2018), and multi-species REM (Wearn et al., 2022), time to event (TTE) and its variations (Moeller et al., 2018), and camera trap distance sampling (CTDS; Howe et al., 2017).

Common to the more recent of these methods is the requirement to estimate the distances and angles from the camera trap to the locations of detected animals. Various methods have been developed for this, such as tracking animal movements on the images based on nearby landmarks (Rowcliffe et al., 2011) or calibration imagery (Henrich et al., 2023; Wearn et al., 2022), using a physical cane grid (Caravaggi et al., 2016), or using poles along the midline of the field of view (FOV; Hofmeester et al., 2017; Mason et al., 2022). All of these methods require extra equipment to be transported to the field, and/or considerable extra time spent analysing images and setting up camera sites. As a result, the uptake of these methods has not been high. This highlights a clear requirement for a method of distance estimation that is easy to implement and straightforward to analyse.

Recent works addressing the efficiency of distance estimation include the use of virtual distance grids laid over the landscape (McKaughan et al., 2023) and a semi-automated distance estimation method requiring calibration for each camera site (Haucke et al., 2022; Henrich et al., 2023). Meanwhile, the fully Automated Distance esTimation (AUDIT) method (Johanns et al., 2022) simplifies both processes of camera site preparation and distance estimation using machine learning algorithms. AUDIT achieved a Mean Absolute Error value of <1 metre during testing, building the case for methods requiring no alteration of camera sites. This has great promise but will require extensive testing to ensure generality; currently, it has been developed to work with video data capture. As a result, advances in streamlined methods for manual distance estimation remain relevant.

Here, we show how Optical Camera Trap Distance Estimation (OCTDE)—a method to estimate detection distances and angles based on optics theory—can be applied to estimating population

density. OCTDE estimates detection distance based on the size of the captured subject on the image. Like AUDIT, this approach—assuming that it provides accurate estimates—allows for a simpler and more convenient site setup than existing alternatives, requiring no extra equipment besides the cameras. This can reduce the manpower and time needed to set up camera trap studies of species density.

To establish the viability of OCTDE, we began with a preliminary assessment on human subjects. Then, we assessed the performance of OCTDE on two South African species by comparing it to an established alternative, based on a virtual distance grid method (McKaughan et al., 2023). We then applied OCTDE to estimate the density of a Hungarian wild boar (*Sus scrofa*) population. We chose wild boars because there is an increased interest in them, owing to the spread of African swine fever (ASF), a highly contagious disease resulting in an almost 100% mortality rate in domestic pigs (Galindo & Alonso, 2017; Quembo et al., 2018). Better approaches for monitoring boar populations are needed and camera trapping is one of the strongest candidate methods (Guerrasio et al., 2022; Palencia et al., 2023). With this set of studies, we aim (1) to build a case for the use of OCTDE as a less resource-intensive method of distance estimation for unmarked animals to support the measurement of population density and (2) to provide comparative data to aid with the development and generalisation of proposed monocular depth mapping.

2 | MATERIALS AND METHODS

Optics theory can be used to estimate the distance of an object to the camera in a given image, if the following information is available: focal length; the object's real-life size (i.e. any linear dimension); and the object's size on the sensor (Leorna et al., 2022; Zuleger et al., 2022). The latter value can be calculated from the object's size on the image in pixels and the size of the sensor in both pixels and millimetres (Greivenkamp, 2004; Hecht, 2012). Specifically, the object's size on the sensor, s (in mm), is given by:

$$s = (S_s \times H_p) / S_p \quad (1)$$

where S_s and S_p are the sizes of the sensor in mm and pixels, respectively, and H_p is the size of the object on the sensor in pixels. Given s , the distance to the object, d (in m), can be calculated as:

$$d = (O_s \times f) / s \quad (2)$$

where O_s is the size of the object in m (estimated based on literature or prior measurements of the population), and f is the focal length of the camera in mm.

The variables required for OCTDE are relatively straightforward to obtain, since sensor size and focal length specifications are usually available in the metadata of images, online, or provided by the manufacturer. If unavailable, these metrics can be estimated for each axis using the equations above and images taken of an object of known size and at known distance from the sensor. Since field of

view estimates were already available in our case, sensor size on the x axis was calculated using:

$$S_s = \tan(\alpha/2) \times d / S_p \quad (3)$$

where α is field of view in degrees, d is distance in m, S_s and S_p are the sensor size in mm and pixels, respectively. S_s for the y axis was calculated using simple proportioning of the known variables of S_s on the x axis and S_p on both axes.

The size of an object on the image in pixels can be measured with most types of photo editing software, for example, by using the Ruler tool in Adobe Photoshop. The only unknown variable is the real object size in the image, which differs for every photographed individual. However, if average measurements of animals in a given population are known or can be obtained from published data, and images are assumed to be unbiased for subject size, it follows that the theory can be used to estimate distance by Equation 2.

Across all experiments, we used Browning Strike Force HD Pro and Browning Strike Force HD Pro X and the field of view estimates (42.5° and 43.7° respectively) were based on data from TrailCamPro (<https://www.trailcampro.com>). The estimates available on the website were verified to be reasonable and within the standard error range of our measurements. All data analyses were carried out using R (Version 3.6.1) (R Core Team, 2018), with the package "Distance" (Miller, 2020) and the camera trap analysis code available at <https://github.com/MarcusRowcliffe/distanceDF> used to estimate density.

2.1 | Preliminary tests of estimating the density of a model population

Initially, six Browning Strike Force HD Pro camera traps were deployed in random locations within a woody area of c. 2 ha in the City of Durham, UK. As the experiment was carried out on the private grounds of the University of Durham, no permission for fieldwork was needed. On triggering, the camera traps were set to take 3 images with a 2 s delay between each frame. Human subjects were used, as they could be instructed to move continuously through the study area over 30 min, without leaving it. The subjects' average height was 180 cm, with a standard error of 1.41 cm. Measurements of object size in pixels were taken using Adobe Photoshop's Rectangular Marquee tool (version: 21.0.2). If the participants were visible on the images in their entirety, height was used to estimate distance. Otherwise, smaller parts of the body were measured, and height was extrapolated from these measurements using established anthropometric proportions (Govind, 2012). Angles of detection were estimated for every image using the camera traps' field of view of 42.5° and the distance of the centre of the subject's body from the midline of the image.

The R package "Distance" calculates effective detection distances (r) and effective detection angles (π) by fitting models to the number of sightings at various distances and angles, respectively. The estimate of overall effort is

$$E = \theta / (2\pi) (T_p / t) \quad (4)$$

where θ is the effective detection angle in radians, T_p is cumulative time spent active across all camera traps, and t is the time between sampling instances (Howe et al., 2017). Activity can also be factored into the estimation of effort (Rowcliffe et al., 2014), but activity was constant in this pilot study. Density is then calculated with the following equation:

$$D = R / (r^2 \pi) (1/E) \quad (5)$$

where D is the density per km², R is the number of sightings, r is the effective detection distance in km, and E is the effort calculated in Equation 4 (Howe et al., 2017). Figure 1 summarises the steps of the OCTDE process, covering data collection, analysis, and subsequent density estimation.

2.2 | Comparing distance and density estimates from OCTDE and virtual distance grids

Data used for this assessment came from a camera trap survey conducted in South Africa in 2019 (McKaughan et al., 2023). Camera traps were spread across 192 km² of the Alldays area, Limpopo Province, South Africa, 60 km south of the intersection of the South African, Botswanan, and Zimbabwean borders. Twenty-five camera traps (Browning Strike Force HD Pro) were deployed at the intersections of a grid with 3 km spacing with a random origin, superimposed over the study site. On triggering, the camera traps were set to take 6 images with a delay of 0.3 s between each frame and 1 s before a new trigger event could occur. Deviations from the grid were allowed, in order to find a tree on which the cameras could be mounted; only one camera was placed further than 30 m from its designated intersection (78 m away). Cameras were set at 0.7 m above-ground, angled parallel to the ground and faced north. A variation of $\pm 30^\circ$ from north facing was allowed, so that the cameras were not facing directly at an obstacle, but only two cameras were not facing directly north.

Cameras remained active for 90 days, from the 1 June to the 29 August in 2019. The 90-day study period ensured that data collection was maximised for the subject species but minimised violations of the assumptions of closed populations (Karanth & Nichols, 1998; Kelly & Holub, 2008) and potential effects of environmental changes due to seasonality. Due to theft, or wildlife affecting camera traps, some camera traps had a smaller window of operation; this was accounted for when calculating survey effort. Across all camera traps, the cumulative number of camera days was 2047.4 (minimum 50.2 days for a single location).

Population densities of two relatively common meso-carnivores, African civet (*Civettictis civetta*) and black-backed jackal (*Canis mesomelas*) were estimated using OCTDE. OCTDE requires linear dimension estimates of various body parts of the studied species. All average metrics for both species were based on estimates from previous literature. For civets, the average shoulder height was estimated to be 40 cm (Shorrocks & Bates, 2015). On a single close-up image, 5 cm was used as the average ear length. This metric was

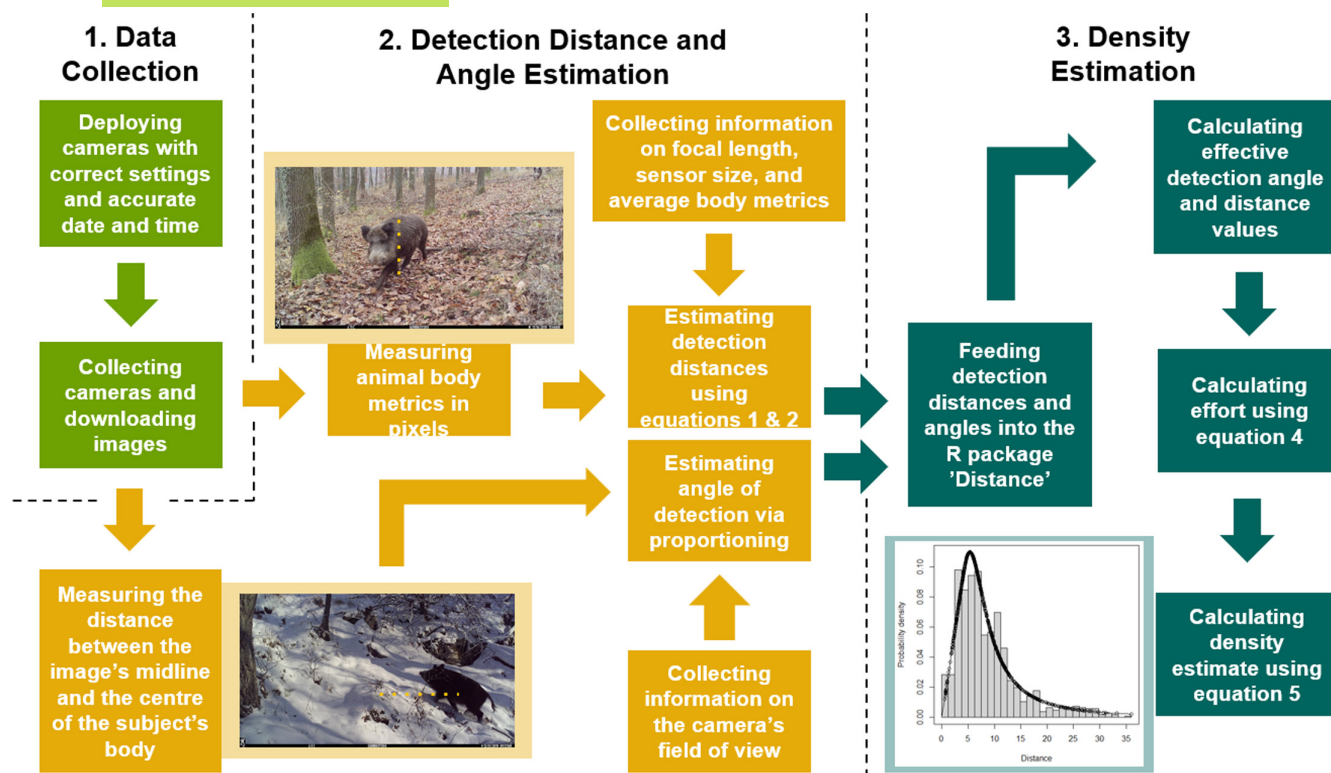


FIGURE 1 Summary of the steps making up the OCTDE process. Yellow dotted lines are schematic examples of the measurement process.

chosen to be just below the range identified by Ray (1995) for adult civets, to account for the inclusion of younger specimens. For jackals, the metric used for shoulder height was also 40 cm, which is within the ranges reported by Walton and Joly (2003) and Stuart and Stuart (2015). This metric was used for the vast majority of cases but, in a few instances, estimations were based on ear (11 cm) and tail (32 cm) measurements (Walton & Joly, 2003). To assess the sensitivity of the density estimate to average metrics assumptions, population densities were estimated in two separate analyses. First, to assess the impacts of error in our size metrics, we repeated all analyses assuming average size metrics were over- or under-estimated by 12.5%. Second, to assess the impacts of interspecific variation in size, we repeated the analyses 100 times, each time drawing the body size metric independently for each observation from a normal distribution with a mean equal to the average dimensions used, but a coefficient of variation of 6.25%.

The same dataset was also analysed using distances estimated using reference pictures taken in the field, with a distance overlay grid (McKaughan et al., 2023). The grid was created using an identical setup to the cameras in the field in a flat and open area, with markers at 1 m intervals used to create a reference image of distances that could be overlaid on each camera trap photo. For each camera, the grid was then adjusted to the location's landscape using a distance marker at 3 m and another, at most, 10 m from the camera, before distances of animals in images were recorded. Distance and density estimates obtained by the two methods were compared. For these comparisons, observations in the '>25 m' category using

distance grid estimates were discarded in statistical analyses for both species, owing to the difficulty of distinguishing distances over 25 m using that method.

To explore why the distance estimates derived from the two methods differed, sightings where the difference between estimates was greater than 5 m were investigated for common features that could introduce biases. A distance of 5 m was selected because some established distance estimation methods work with 2.5 m distance bins (Hofmeester et al., 2017). By analysing cases with differences in estimates larger than 5 m, we could be sure that at least one of the methods' estimates differed by more than 2.5 m from the true distance.

2.3 | Estimating wild boar density in Bükk National Park

Bükk National Park (423 km²) in north-eastern Hungary is in the most mountainous region of the country. It is densely forested and features karst formations, such as large caves, swallow-holes and ravines. In 2019, as part of MammalNet Hungary, the Hungarian branch of a European volunteer-based camera trap network (Smith et al., 2023), officers at Bükk National Park (BNP) were given six Browning Strike Force HD Pro X camera traps and associated equipment. As the deployment of the cameras was part of the officers' standard daily operations, no additional permission for fieldwork was needed for the study. On triggering, the camera traps were set

to take 3 images with a 0.3 s delay between each frame. Our study used data collected between October 2019 and March 2020.

Staff at BNP were free to use the camera traps as they wanted but were told not to use baits when trapping and not to deliberately place camera traps next to nests or feeding stations; these instructions were intended to avoid bias in estimates (Foster & Harmsen, 2012). The six camera traps were spread out across the National Park and were active for a cumulative total of 452.4 camera days. Wild boar linear measurements were based on 248 wild boars from three Hungarian game farms: 72.6 cm for withers height, 12.5 cm for ear length, and 44.6 cm for head length (Bodnár et al., 2015).

3 | RESULTS

3.1 | Estimating density of a model population

The woodland study of human density yielded 94 images containing subjects. Given the number of participants (5) and the size of the area (19,797 m²), the true density was 252.6 people per km². For calculating θ (the effective detection angle), distance sampling algorithms selected the half-normal key function, and the estimate was 42.4° (± 20.65 SE), due to the lack of a significant drop in the number of observations towards the edge of the field of view (Figure 2a). For calculating r (the effective detection distance), the hazard-rate key function was selected, and the estimate was 14.58 (± 0.80 SE) m (Figure 2b). The estimated density using OCTDE was 265.65 (± 142.14) people per km². Despite the very high uncertainty, the point estimate is very close to the actual value.

3.2 | Density estimates from OCTDE and distance grids on South African civet and jackal populations

Left truncation can help realise the assumption that detection probability is certain at the lowest detection distance. From the left, any observations at shorter distances than the first observation category with 0 observation events were discarded, if the images amounted to less than 5% of all data from the camera site. The civet dataset was truncated at 2.5 m from the left and 18 m from the right,

while the jackal data were truncated at 1.5 m from the left and 24 m from the right. Truncation resulted in a loss of approximately 5.3% of civet and 3.6% of jackal observations. The frequencies of different detection distance angles and estimates (Figure 3) were used to estimate θ and r , respectively.

In the case of both species, half-normal key functions were used for calculating θ , and hazard-rate key functions for calculating r . Those, in turn, were used to estimate densities for each species (Table 1). Design-based standard error values (Dunning, 2010; Howe et al., 2017) derived using the Delta method (Seber, 1982) are provided for all estimates. The method used CVs from (1) detection probability (which encompasses the uncertainty of effective detection distance), (2) the encounter rate, (3) the activity multiplier, and (4) the effective detection angle multiplier; the encounter rate accounts for 99% of the variability. Tables 2 and 3 show the results of testing the sensitivity of population density values to changes in assumptions for average body metrics of the subject species.

3.3 | Comparing distance estimates from OCTDE and distance grid

Linear models of OCTDE distance estimates as a function of distance grid estimates had non-zero intercepts and slopes of less than 1.0 (Table 4). This was because although the two measures were strongly positively correlated for distances relatively close to the camera, that positive relationship was lost further from the camera. In fact, a segmented linear relationship provided a better fit to the data across both species (Figure 4, Table 5). The breakpoints between the slopes in the segmented regression are approximately 8 m for the civet and 12.5 m for the jackal. The initial slopes were larger than 1, while the second slopes were nearly 0 for both species.

Also, 264 (of 1527) comparable observations across the two species displayed a difference of more than 5 m between the estimates. Out of the 25 camera traps, a non-level horizon on the images was seen in seven, suggesting some degree of tilt. 250 (95%) of the 264 observations with large differences in estimates were derived from these seven camera traps.

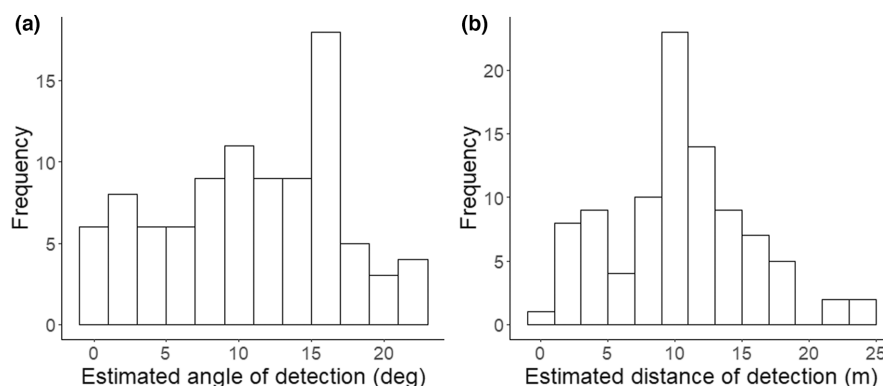


FIGURE 2 Distributions of the angle of detection (a) and detection distance (b).

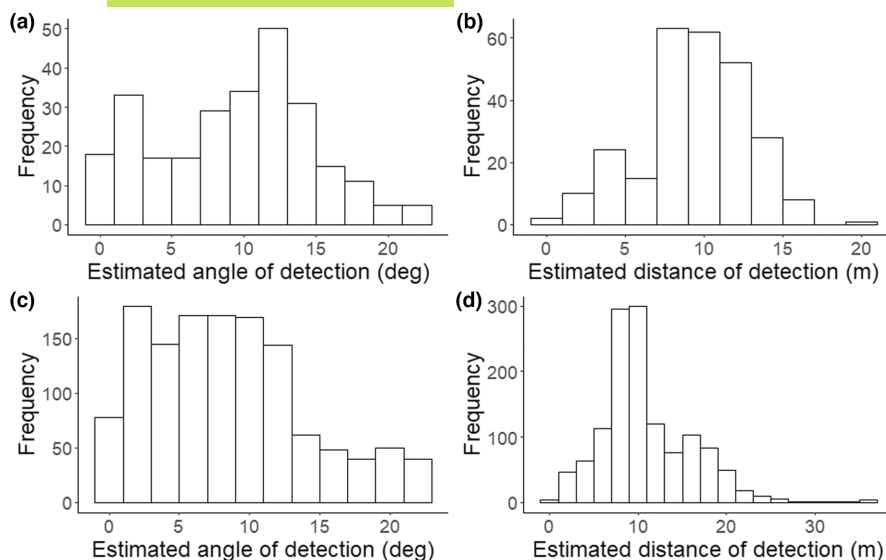


FIGURE 3 Frequency of observations by the angle of detections and detection distances for civet (a and b, respectively) and jackal (c and d, respectively).

TABLE 1 Effective detection angle (θ) and effective detection distance (r) and values from OCTDE analysis and the results of both OCTDE and the distance grid method by species.

Species (number of observations)	Effective detection angle ($^{\circ}$)	Effective detection distance (m)	OCTDE population density estimate (/km ²)	Distance grid population density estimate (/km ²)
African civet (265)	31.92 (± 2.20 SE)	13.46 (± 0.26 SE)	0.074 (± 0.079 SE)	0.108 (± 0.06 SE)
Black-backed jackal (1297)	28.89 (± 0.70 SE)	13.58 (± 0.24 SE)	0.325 (± 0.192 SE)	0.365 (± 0.150 SE)

TABLE 2 Density estimates of jackals and civets using OCTDE, with average, 12.5% larger and 12.5% smaller body metrics.

Species (number of observations)	OCTDE population density estimate using +12.5% assumed body metrics (/km ²)	OCTDE population density estimate using average metrics (/km ²)	OCTDE population density estimate using -12.5% assumed body metrics (/km ²)
African civet (265)	0.059 (± 0.062 SE)	0.074 (± 0.079 SE)	0.097 (± 0.103 SE)
Black-backed jackal (1297)	0.257 (± 0.152 SE)	0.325 (± 0.192 SE)	0.423 (± 0.250 SE)

TABLE 3 Summary of 100 density estimates of jackals and civets using OCTDE while generating a different assumed body metric for each individual observation. Each metric was randomised using a normal distribution with a standard deviation of $\pm 6.25\%$ around the average metric.

Species (number of observations)	Minimum OCTDE population density estimate (/km ²)	Mean OCTDE population density estimate (/km ²)	Maximum OCTDE population density estimate (/km ²)
African civet (265)	0.069 (± 0.074 SE)	0.075 (± 0.080 SE)	0.080 (± 0.085 SE)
Black-backed jackal (1297)	0.321 (± 0.190 SE)	0.326 (± 0.193 SE)	0.330 (± 0.196 SE)

TABLE 4 Linear regression analysis of the distance estimates from OCTDE and Distance Grid. Selected models, based on AIC, are in bold.

Species (number of observations)	$y = ax + b$ AIC	$y = ax$ AIC	Intercept ($\pm$ SE)	Slope ($\pm$ SE)	R^2 of trendline	R^2 of $x = y$
Civet ($n = 265$)	1325.0	1435.8	5.291 (± 0.448)	0.455 (± 0.045)	0.278	-0.131
Jackal ($n = 1262$)	6986.8	7188.5	4.025 (± 0.271)	0.672 (± 0.025)	0.359	0.245

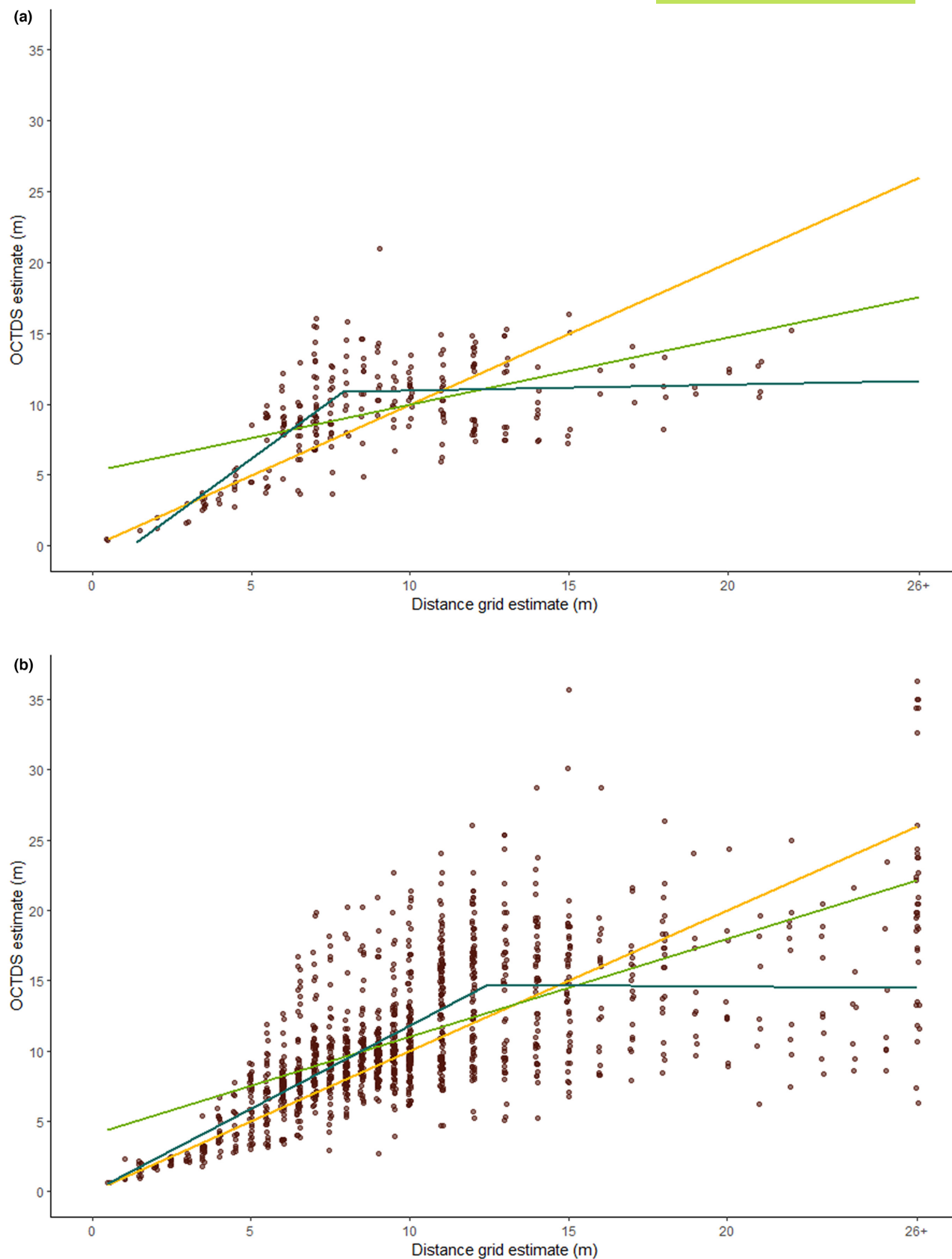


FIGURE 4 Relationship between distance estimates for (a) civet and (b) jackal using OCTDE and the distance overlay grid. Points represent individual observations. The orange lines represent an ideal 1:1 ratio between the two factors, where all objects are estimated to be at the same distance by the two methods. The green and blue lines are models describing the observed relationship between the two variables using linear regression and segmented regression, respectively. Models were fitted by excluding observations in the >26+ category on the x-axis.

TABLE 5 Segmented regression analysis of the distance estimates from OCTDE and Distance Grid. Selected models, based on AIC, are in bold.

Species (number of observations)	$y = ax + b$ AIC	$y = ax$ AIC	Intercept ($\pm$ SE)	First slope ($\pm$ SE)	Break-point ($\pm$ SE)	Second slope ($\pm$ SE)	R^2
Civet ($n = 265$)	1225.8	1230.4	-2.073 (± 0.845)	1.641 (± 0.139)	7.882 (± 0.296)	0.037 (± 0.152)	0.511
Jackal ($n = 1262$)	6780.4	6778.7	N/A	1.178 (± 0.013)	12.482 (± 0.321)	-0.016 (± 0.067)	0.901

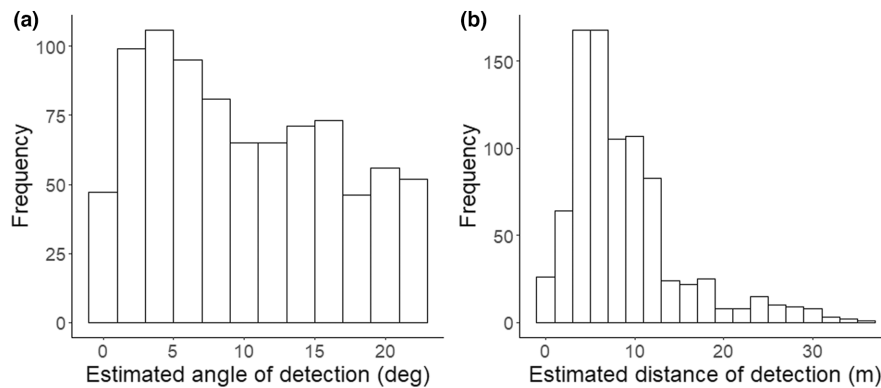


FIGURE 5 Histograms of the number of wild boar observations by the angle of detections (a) and detection distances (b).

3.4 | Estimating wild boar density in Bükk National Park

Here 856 observations of wild boars were obtained. Using the half-normal key function with cosine (2) adjustments we estimated $\theta = 38.35^\circ (\pm 1.31 \text{ SE})$, due to a decrease in the number of observations towards the edge of the field of view (Figure 5a). Using a hazard-rate key function, we estimated $r = 9.26 (\pm 0.24) \text{ m}$ (Figure 5b). The estimated density using OCTDE was $0.480 (\pm 0.35 \text{ SE})$ wild boar per km^2 .

4 | DISCUSSION

Generally, the development, testing, and application of OCTDE highlights its potential as a viable tool for efficiently estimating distances of animals in camera trap images, with important insights gained across all three studies. Here, we discuss the performance of our method, its limitations, strengths, future potential, and implications for wild boar population density in Bükk National Park, Hungary.

4.1 | Testing OCTDE in the field

In the human trial, the density estimate obtained using OCTDE was extremely close to the actual value. As with many applications of camera trap density estimation, the standard error of the estimate was very large. This is likely to have arisen because of the very short trial and the small number of camera traps. A longer trial and more camera traps would have yielded a larger number

of detections from a wider spread of sampling locations and thus greater precision.

When we applied OCTDE to data on jackal and civet populations in South Africa, the resultant point estimates of density were close to the estimates derived from the distance grid-based method for both species. The estimates are also realistic compared to generally reported densities. Civet and jackal density estimates generally fall between $0.003\text{--}0.1/\text{km}^2$ (Mullu & Balakrishnan, 2014; Rich et al., 2019) and between $0.31\text{--}22/\text{km}^2$, respectively, in African studies (Bingham & Foggin, 1993; Hiscocks & Perrin, 1987; Jenner et al., 2011; Rowe-Rowe, 1982). For both species, our OCTDE density estimates are within the reported ranges, suggesting that—although, in the absence of knowledge of the ‘true’ densities in our study area, we cannot state with confidence that they are accurate—they are certainly plausible (McKaughan et al., 2023).

Although the density estimates from the two methods were similar, there were differences in the precise distance measurements. The segmented regression analysis for both species suggested a plateauing of the relationship between OCTDE and inferred distance overlay grid estimation above threshold distances (8 and 12 m, respectively, for civet and jackal). The presence of these plateaus suggests that, once the animal is above a certain distance, at least one of the methods has very little capacity to differentiate distances accurately. Both approaches rely on the accuracy with which image subjects can be treated, and reductions in image fidelity with increasing distance from the camera mean that, the further the subject is from the camera, the lower the information content of the image. With OCTDE, a large difference in estimated distance can result from a small difference in measured height in pixels when the animal is far away, due to the exponential relationship between estimated distance and pixel size. Similarly, the resolution of the distance grid drops exponentially as the subject gets further away

from the camera. Both methods have sensitivity to radial distortion towards the edges. This effect is relatively small due to the narrow field of view of the camera traps but could be corrected in future studies using software, such as OpenCV (Hartley & Kang, 2007; Lee & Hua, 2014).

Based on the comparison alone, it is not possible to tell which method of distance measuring is more accurate. Variance in subject height can introduce bias in the case of OCTDE. On the other hand, the distance grid can become very inaccurate if the camera is slightly tilted around the roll axis (Figure 6) by animals, by environmental forces, such as rain or wind, or when initially mounted. This can lead to inferred grids not being completely parallel with the ground, which results in an overestimation of the distance on one side of the image and underestimation on the other. Horizontally sloping terrain will also decrease the accuracy of distance grids. When assessing the images, it is relatively easy to determine whether camera tilt might be responsible for errors in distance estimation, but much harder to say whether those errors might have arisen because the animal was of atypical size. Focusing on the former explanation, therefore, images with distance estimate discrepancies were assessed to determine whether camera tilt might be responsible for the observed discrepancies.

Because 95% of images with a difference in distance estimates of more than 5 m were derived from camera traps with a non-level horizon, and because the size of the subjects on the images (and thus OCTDE distance estimates) are unaffected by tilt around the roll axis, most cases of strongly differing estimates could plausibly be attributed to limitations of the distance grid method. Thus, whilst inaccuracies of OCTDE are hard to estimate from the data, since the true height of the individual subjects is not known, the large discrepancy in some estimated distances is not necessarily attributable to inaccuracies in OCTDE.

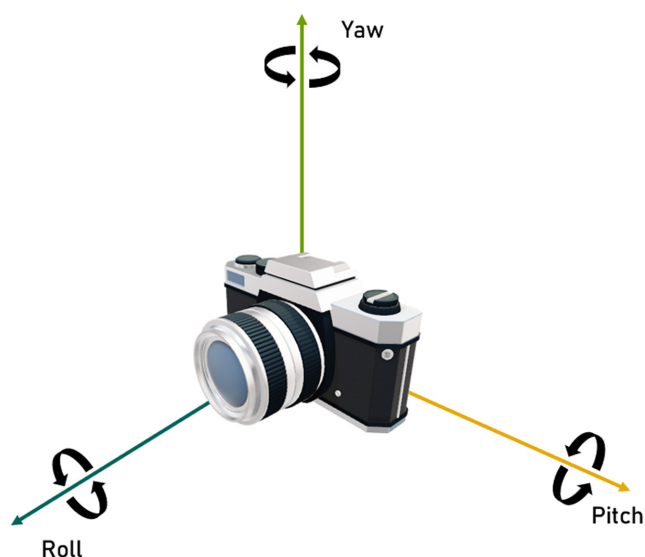


FIGURE 6 The three axes of tilt of an object. The comparison of the virtual grid method and OCTDE identified a high sensitivity of the former to tilt around the roll axis.

Despite the reassurance provided by our checks for camera tilt, it remains likely that some of the discrepancies between distance estimation methods will be attributable to an error in assumed body sizes used in OCTDE. In the case of jackals, uncertainty in height measurements is around 25% (Sheldon, 1992). Since the assumed average body metric values are important inputs for the model, the effect of change in these metrics was tested. Increasing the jackal and civet body length metrics by 12.5% led to decreases of around 20% in density estimates, whilst decreasing assumed body size metrics by 12.5% led to increases of around 30% in density estimates (Table 2). This emphasises the importance of accurate estimation of body sizes. However, it also suggests that quite large errors in assumed body sizes can still give useful inferences of population densities. Even with a 25% (relatively broad) difference between the minimum and maximum body size measurements, minimum and maximum estimates displayed smaller than two-fold differences. Owing to our large sample sizes, density estimates from assigning different assumed body metrics, drawn from a normal distribution, to individual detection events did not deviate from those derived by assuming the average metrics. This result suggests limited impact from the uncertainty of body sizes when individuals are of reasonably similar size (i.e. outside of periods when juveniles are still substantially smaller than adults) but the average metrics are accurately estimated.

4.2 | Using OCTDE to estimate wild boar density in Bükk National Park

Wild boar population density was estimated to be 0.480/km² by OCTDE in the research area. Populations of wild boar in western Eurasia generally occur at densities between 0.01 and 10 individuals per km² (Melis et al., 2006). The most recent estimate of wild boar population density in the area comes from a report produced by the Hungarian Ministry of Agriculture (2018), stating that the wild boar population has surpassed 2–3 boars per km² in a 'significant part' of BNP. Over 1000 wild boars were shot throughout the culling season of 2019, across the National Park (P. Gombkötő, BNP zoologist, pers. comm.), equivalent to 2.36 boars per km². Although the population had some potential for recovery before our survey, deforestation and burns, the spread of large carnivores, and large-scale building of fences in the study area could limit this. Our density estimate is highly plausible in this context.

While the aim of this study was to explore the application of OCTDE, the approach of selecting camera trap locations was not systematic, which could bias our estimates. This approach was used because the establishment of citizen science projects requires a balance between the ease of participation and the rigour of required actions (Wiggins & Crowston, 2011). The requirement for systematic randomisation of site locations by volunteers would have been hard to verify and could also deter them from participating. With large enough engagement in the country, the sampling effort might allow the potential biases of non-randomised

camera placement (Cusack et al., 2015; Steenweg et al., 2016) to be assessed and controlled for.

While our results are limited to Bükk National Park for a period between October 2019 and March 2020, data collection from three Hungarian National Parks as part of MammalNet Hungary and various other countries across Europe (www.mammalweb.org) is ongoing. Camera trapping datasets are providing opportunity for retrospective analysis with OCTDE allowing deeper understanding of ecological processes. The density estimate here serves as a preliminary baseline for future studies of the region and ongoing study could provide a clearer understanding of the effects of African swine fever on wild boar populations in Central-Eastern Europe.

4.3 | The future of OCTDE

The main limitation of OCTDE stems from the use of average size metrics to estimate all distances. Our brief sensitivity assessment suggests that significant departures from an accurate estimate of average dimensions can still yield useful density estimates (well within the range of uncertainty of most published estimates for the density of wild populations; Bessone et al., 2020; Cappelle et al., 2019; McKaughan et al., 2023); however, the extent to which body size variation within a population affects distance and subsequent density estimations is yet to be studied. Different sex and age categories present a particular problem, especially given that age composition will vary seasonally for many wildlife populations. Given the large size differences between male and female adults, yearlings and juveniles, this is a particular concern for wild boar. This issue could be minimised by using a different set of metrics for juveniles or by omitting them from studies. However, the identification of age (or sex) classes is a difficult and inexact process for many species and is even harder when done through camera trap images. It is also expected that the body posture of the observed individual and its alignment with the camera trap could affect the results of distance and subsequent density estimations; these effects remain to be quantified.

Despite the obvious complexities of applying OCTDE in heterogeneous populations, this method has many advantages over those previously established. Firstly, apart from the camera trap, no extra equipment, such as cane grids (Caravaggi et al., 2016) or poles (Hofmeester et al., 2017; Mason et al., 2022), is needed when setting up a new camera site (although they can be used to support OCTDE by generating study-specific average size metrics). This is not only beneficial for making the standardisation and logistics of studies easier, but it also eliminates some weak points in study design, since cane grids and poles can be broken or knocked over by animals. This allows OCTDE to be applied efficiently in difficult environments, such as marshlands or mountainous setups, where the placing of markers is not feasible. Furthermore, the simplification of setting up a camera site even when compared to methods requiring calibration (Haucke et al., 2022; Henrich et al., 2023; Wearn et al., 2022) makes the process less cumbersome, which can increase community engagement (Wiggins & Crowston, 2011). This can help

solve the recent issue of volunteers becoming increasingly hard to enlist in citizen science projects (Willi et al., 2019), which is—otherwise—a promising approach to tackling the problems of data collection in large-scale camera trap studies (Hsing et al., 2022; McShea et al., 2016; Swanson et al., 2015). While recently proposed automated alternatives (Johanns et al., 2022) are exciting and offer hope, they are at an early stage of development, with little assessment of generalisability (Rees, 2023). Meanwhile, the simplicity of OCTDE suggest that it should be applicable across a wide variety of species in multiple types of environments, while producing results of similar accuracy and robustness. OCTDE can also be used in established datasets retrospectively, while that is not the case for automated methods like AUDIT, or methods requiring calibration or extra equipment at camera sites.

Another advantage of OCTDE is that, based on our experience, analyses are quick relative to, for example, mapping the movement of animals based on the nearby landmarks in each camera site (Rowcliffe et al., 2011). This can save time and resources in surveys. Since this has not been quantified experimentally, it would be worthwhile to measure the amount of time saved during analysis with OCTDE compared to other methods. A third advantage is that this method is relatively robust to changes in camera view or height, and tilts around the yaw and roll axes (Figure 6), because the known size of a focal object will still indicate its distance from the lens. Of course, changes in tilt around the pitch axis would require additional adjustments for estimations, as the 'keystone distortion' caused by this type of tilt would affect the relationship between distance and the number of pixels covered by an object. The required adjustments would be specific to camera specifications, but methods are available to correct for the 'keystone distortion' effect (Liu et al., 2019). In most cases, however, significant tilting around the pitch axis would stop the data collection process (as the frame would show the ground below or the sky above the camera site) and therefore its implications were not explored further. Finally, a potential advantage of OCTDE over the distance grid option is that sizes can be estimated even when the subject is over 25 m away. For example, using the Browning Strike Force HD Pro with a resolution of 2080×3744 pixels, an average jackal 25 m away would be 77 pixels tall, while 30 m away, it would be 64 pixels tall. This is still a substantial difference, which could be further improved with increased fidelity of the images.

Validation for OCTDE beyond this paper is derived from previous tests of its photogrammetry (Leorna et al., 2022; Zuleger et al., 2022) and population density estimation approaches (Howe et al., 2017). Here, it was tested on a model population of known size and compared to an alternative method that also has associated uncertainty. The results from these tests showcase the potential of OCTDE, but further research is needed on the propagation of uncertainty when using the method. One example would be taking images of individual animals of known body size metrics at various distances and trying to estimate these distances. A study like this could shed light on the effects of variance in body size and posture on distance estimates. Estimating densities of populations of known abundance would also be useful to further probe the accuracy of OCTDE. Further comparisons with other

distance and density estimation methods could increase our understanding of the advantages and disadvantages of OCTDE.

We tested OCTDE's applicability in a complete density estimation method, mostly based on CTDS (Howe et al., 2017), and found that it provided an efficient process of distance estimation of observations for the calculation of effective detection distance. Consequently, this approach is also applicable to any other density estimation methods requiring or benefiting from an effective detection distance value, such as REM (Rowcliffe et al., 2008). Further research could usefully assess how OCTDE can be complemented with methods relying on physical objects in the camera site (Caravaggi et al., 2016; Hofmeester et al., 2017; Mason et al., 2022; Rowcliffe et al., 2011) to achieve the optimal balance between practicality and accuracy.

OCTDE has significant potential for exploitation in animal density estimation, due to its practicality both in the field and during data analysis. Furthermore, since OCTDE does not have special requirements for setting up camera sites, it could be used for retrospective analyses on a large number of already existing datasets. Before that, however, OCTDE would need to be tested in a wide range of subject species and environments, to determine its true utility. Hopefully, it will become another tool in the toolbox of ecologists and conservationists.

AUTHOR CONTRIBUTIONS

Bálint Ternyik and Philip A. Stephens conceived and designed the study. Bálint Ternyik and Jamie E. T. McKaughan collected and analysed the data. Bálint Ternyik wrote the paper with editorial oversight from Philip A. Stephens, Jamie E. T. McKaughan, and Russell A. Hill.

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CONFLICT OF INTEREST STATEMENT

Between the beginning of the study and the publication of its findings, Bálint Ternyik was employed by PwC and later by UNEP-WCMC.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Images, analysis code and measurements for the human trial and the wild boar study are available on OSF: <https://doi.org/10.17605/osf.io/G6TH4> (Ternyik & McKaughan, 2023), along with analysis code and measurements for the jackal and civet experiments.

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