Towards a best-practices guide for camera trapping: assessing differences among camera trap models and settings under field conditions

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Abstract

Camera trapping is a widely used tool in wildlife research and conservation, and a plethora of makes and models of camera traps have emerged. However, insufficient attention has been paid to testing their performance, particularly under field conditions. In this study, we have comparatively tested five of the most frequently used makes of camera trap (Bushnell, KeepGuard, Ltl Acorn, Reconyx and Scoutguard) to identify the key factors behind their probability of detection (i.e. the probability that the camera successfully capturing a usable photograph of an animal passing through the field of view) and trigger speed (i.e. the time delay between the instant at which a motion is detected, and the time at which the picture is taken). We used 45 cameras (nine devices of each make) with infrared flash in a field experiment in which a continuous remote video was used in parallel (as a gold-standard) to discover the animals that entered the camera trap detection zone. The period (day/night), distance between animals and cameras, model, species, deployment height and activation sensitivity were significantly related to the probability of detection. This probability was lower during the night than during the day. There was a greater probability of detecting a given species when the cameras were set at its shoulder height. The interaction between species and the distance between the animals and the cameras significantly affected the trigger speed, meaning that the closer the animals that entered the detection zone, the higher the trigger speed, with substantial differences among species. This was probably related by movement speed. In conclusion, this study shows differences in the performance of camera trap models and settings, signifying that caution is required when making direct comparisons among results obtained in different experiments, or when designing new ones. These results provide empirical guidelines for best practices in camera trapping and highlight the relevance of field experiments for testing the performance of the camera traps.

Introduction

The use of autonomously triggered cameras (camera traps) for wildlife research has exploded since 2000 (Burton et al., 2015). Camera trapping is widely used extensively in terrestrial vertebrate research for a wide range of purposes, including species inventories (Tobler et al., 2008), abundance and density estimates (Gilbert et al., 2021), and movement and behaviour studies (Caravaggi et al., 2017; Niedballa et al., 2019). Camera trapping can be carried out at a relatively low cost (barring the initial purchase), it is minimally invasive, and makes it possible to monitor elusive species and/or remote areas (Rovero & Zimmermann, 2016).

The wide range of applications has led to the emergence of a plethora of camera trap makes and models during the last

few years. These makes differ as regards their features, specifications and costs (Rovero & Zimmermann, 2016). This wide range of camera traps signifies that a rigorous way in which to test their performance is required to integrate the data from different experiences and thus to carry out effective wildlife management and conservation programmes, since there are still several issues regarding the use of camera traps (Delisle et al., 2021; Glover-Kapfer et al., 2019). Some studies have indicated the malfunctioning of camera traps and the high variability in performance among makes and devices in terms of missed detections (Hofmeester et al., 2019; Jacobs & Ausband, 2018; McIntyre et al., 2020). For instance, some authors have described factors affecting the performance of cameras, such as (1) environmental conditions, that is, humidity or temperature (Jacobs & Ausband, 2018; Kays et al., 2010; McIntyre et al.,

2020; Rowcliffe *et al.*, 2011); (2) target species, owing to body size (Hofmeester *et al.*, 2017) and speed of movement (Rowcliffe *et al.*, 2011) and (3) camera trap deployment and settings, that is, height and sensitivity (Swann *et al.*, 2004). Missed detections could potentially generate misleading results in camera trapping studies, and therefore, create difficulties as regards direct comparison among studies (Jacobs & Ausband, 2018). In this respect, despite some statistical approaches accounting for the imperfect detection (Guillera-Aroita *et al.*, 2010), recent studies have shown that biased and imprecise results can be obtained when detection probabilities are low (Hofmeester *et al.*, 2021; Kays *et al.*, 2021). Additionally, (1) there are a wide variety of studies that used the raw encounter rates without accounting for false-negatives (i.e. those animals/sequences that were not recorded by the camera trap but actually entered the area monitored by the camera, the field of view – FOV). For instance, those focused on species interactions, activity patterns, or inventories, among others and (2) some of the methods that account for imperfect detection assumed certain detectability at some point of the detection zone (e.g. Howe *et al.*, 2017), which could not be always realistic. These reasons signify that assessing the performance of camera traps under field conditions, along with defining limitations and applications, still requires further research (Meek *et al.*, 2015). Understanding the constraints of camera trapping in a broad sense, and for a range of camera trap models, will assist researchers to (1) make decisions about which camera trap and settings are appropriate for a given study; (2) compare the results of studies that use different camera trap models and (3) include uncertainty regarding camera trap detection in subsequent modelling approaches.

However, testing camera traps under field conditions is challenging because it requires a high sampling effort in terms of the time and number of devices required to achieve a useful sample size. It is for this reason that most comparisons have been carried out in laboratory trials and using humans, or even domestic animals, walking in front of the camera traps (Apps & McNutt, 2018; Cusack *et al.*, 2015; Seccombe, 2017; Swann *et al.*, 2004; Yajima & Nakashima, 2021). When wild animals are eventually considered as the target, other difficulties emerge, which are mainly related to false-negatives (Driessen *et al.*, 2017; Hughson, Darby, & Dungan, 2010; Jacobs & Ausband, 2018). Undetected sequences are never quantified, and may therefore lead to an important overestimation of the performance of cameras. For an appropriate validation of the performance of a camera trap, it is mandatory to know the number of opportunities that had to record animals. The assessment, therefore, ideally requires the recording of all the animals that enter the FOV of the camera traps, using an independent device and/or approach.

In this context, the objective of this study was to gain better understanding of the performance of camera traps and to evaluate the key factors that influence their probability of detection (i.e. the probability that the camera successfully capturing a usable photograph of an animal passing through the FOV) and trigger speed (i.e. the time delay between the instant at which a motion is detected, and the time at which the picture is taken). In camera trapping studies, probability of detection is

usually described as a combination of three conditional probabilities. First, the probability that an animal moves in front of the camera; second, the probability that the animal triggers the PIR; and third, the probability that the animal is identifiably detected on an image (Findlay *et al.*, 2020; Hofmeester *et al.*, 2019). Thus, we can separate into availability (first component, was the animal in the area) and detectability (second and third components, did the camera work as expected). In this study, we were focused on the detectability component. Probability of detection and trigger speed are the most frequently demanded technological developments and relate to sensor performance (Glover-Kapfer *et al.*, 2019; Meek & Pittet, 2012). We have therefore tested five different camera trapping models (of five makes: Bushnell, KeepGuard, LtlAcorn, Reconyx and Scoutguard), different settings (sensitivities and period of the day) and deployment characteristics (height) in a field experiment in which wild animals were considered to be the target. We monitored the presence of animals in the FOV of cameras and the adjacent area using an external video camera 24/7 as a gold-standard reference for all the animals that should actually have been recorded by the camera traps.

Material and methods

Study area

The study was carried out in the ICTS (Scientific Technical Infrastructure) of the Doñana Biological Reserve (ICTS-RBD, <http://icts.ebd.csic.es/es/inicio>), a territory of approximately 6800 ha located in Doñana National Park (37°0'N, 6°30'W; DNP). Doñana National Park is one of the most important nature reserves in Europe in terms of biodiversity and was declared a Biosphere Reserve by UNESCO in 1980. The Doñana Biological Reserve is located on the Atlantic coast of south-west Spain and is dominated by Mediterranean shrubland and characterised by seasonal marshland.

Field experiment

Sampling period

The experiment was carried out during a 5-week period in the summer of 2018 (July 13rd to August 19th). The weather during the survey was hot and dry: the average daily temperature was 29.93°C, the average temperature at sunrise was 18.40°C, the average maximum temperature was 32.12°C, and there was no rainfall throughout the survey (data from a weather station located 4 km away from the experiment). These values are within the range of operating environmental weather conditions described by the manufacturers (Table 1).

Experimental design

The experiment took place in the ecotone between marshland and shrubland, close to a natural water hole (Fig. 1). This location was selected so as to detect a high number of species and animals during the survey, since water and grassland are highly demanded resources in the study area during the

Table 1 Key technical specifications of the camera trap models tested in the study. All the parameters included in this table were obtained from the official user manuals, with the exception of the FOV of Reconyx, which was obtained from <https://www.trailcampro.com/products/reconyx-hc500-review#tab2>, since it was not included in the user manual

	BUS	KPG	LAC	RNY	SCT
Lens FOV (°)	42/45 ^a	50	55	42	40
IR – Flash Range (m)	30	12–15	20	15.25	10–12
Trigger time (s)	0.2	1	0.6	0.25	1.2
Trigger interval (s)	1	5	0	RapidFire ^b	1
Operating temperature (°C)	–20 to 60	–20 to 60	–30 to 70	–7 and above ^c	–20 to 60
Storage temperature (°C)	–30 to 70	–30 to 70	NA	NA	–30 to 70
Operating humidity (%)	5 to 90	5 to 90	5 to 95	NA	5 to 90
Cost ^d	€€	€	€	€€€	€

Camera trap model abbreviations: BUS, Bushnell Trophy Cam Aggressor model 119774; FOV, field of view; KPG, KeepGuard 680V; LAC, Ltl Acorn Ltl-5310 Series; RNY, Reconyx HyperFire HC500; SCT, Scoutguard SG550BV. All the cameras were purchased in 2017.

^a42° in French, Spanish, German and Italian sections, and 45° in English section of the same manual.

^bThe manual indicated as far option 'RapidFire'.

^cUsing AA Alkaline batteries.

^d€ (price ranged from 100 to 170€), €€ (price ranged from 220 to 280€), and €€€ (price ranged from 350 to 400€).

Figure 1 Experimental design used in this study. Note the three sampling points, and the wooden sticks defining the distance intervals. The top left-hand corner contains a photo of one of the sampling points.

summer (Barasona *et al.*, 2014; Barroso *et al.*, 2020). The vegetation in front of the cameras was short grass (Fig. 1) and there was no slope.

We tested forty-five camera traps of five different models (corresponding to five different makes, and nine of each device): Bushnell Trophy Cam Aggressor model 119774 (BUS), Keep Guard 680V (KPG), Ltl Acorn Ltl-5310 Series (LAC), Scoutguard SG550BV (SCT), and Reconyx HyperFire HC500 (RNY) (Table 1); all of them used passive infrared motion sensors (PIR) and infrared flash. All the camera traps were programmed to be operative all day, and to record one photo in each activation with the minimum time lapse between consecutive activations. The date and time were automatically

stamped onto each photo. We checked the camera traps twice to change their batteries and memory cards, when necessary, and to ensure that they were functioning correctly. We used the same alkaline batteries in all the camera traps.

We designed an experiment with three spatial replicates (sampling points; Fig. 1). At each sampling point, three camera traps of the same model were placed on the same stick at three different heights from the ground (30, 45 and 60 cm). Camera traps of different models were placed side by side, no more than 10 cm apart, and aligned vertically and horizontally. Three cameras of each model were set to a low, medium and high sensitivity, and the height at which cameras with a given sensitivity configuration was rotated between sampling points.

Wooden sticks were placed to define four 2.5 m wide intervals, from 0 to 10 m, within the FOV of the camera traps (Fig. 1). These sticks were used to delimitate the FOV of each sampling point (i.e. a common detection zone for the 15 camera traps at each sampling point) and were later used to locate the position of the individuals registered. We considered 10 m as maximum distance based on previous studies that reported detection distances for the species sampled in this study (Hofmeester *et al.*, 2017; Palencia, Rowcliffe *et al.*, 2021). The cameras were angled to be parallel to the slope of the ground. This design probably modified the basal encounter rate and behaviour of the animals, but did not introduce bias into our experiment and analysis, as we focused on those animals that entered the FOV and we did not consider their behaviour.

The gold-standard reference for the animals entering the FOV of the camera traps consisted of monitoring the sampled area and surroundings with a video camera that recorded and streamed in a continuous mode (infrared at night) throughout the study period (Appendix S1). This camera was supported by the ICTS-RBD. For each sampling point, we only considered those animals that crossed the centre of the FOV of the central camera trap. We considered this criterion to discard those animals that entered and left on the edge of the FOV of external cameras and could not be potentially recorded for all of them.

Data processing

Video camera

For those animals that entered the FOV at each sampling point, we annotated: the date and time of each sequence, the species and the distance interval of the first animal that entered the FOV. We considered as a sequence every animal or group of animals that entered the FOV. When more than one animal entered the FOV simultaneously, that which was closest to the camera traps was considered to estimate the distance interval parameter.

Camera traps

Camera trapping may generate a high amount of data without information, ‘blank-images’ or ‘false-positives’, because of vegetation, the sun or dappled shade activating the cameras (Glover-Kapfer *et al.*, 2019). All the images recorded were first assessed for the presence of animals, after which they were annotated for each sequence: the date and time, the species and the distance interval of the first and closest animal in the sequence.

Analysis

We first compared the total number of photos (including blank images) recorded by each camera trap as regards sensitivity settings and models. Subsequent analyses were carried out with the information concerning the sequences of animals entering the FOV at a distance closer than 10 m. Two generalised linear mixed models (GLMM) with a binomial distribution and logit

link function were used to assess the performance of the camera traps as regards the probability of detection and trigger speed, respectively. When modelling the probability of detection, our response variable was the detection of each sequence recorded by the video camera (1 recorded by a camera trap, 0 unrecorded). When modelling trigger speed considering only the captures obtained by the camera traps, the response variable was 1 when the camera trap recorded the animal in the same distance interval that it entered, and 0 when it was recorded in another interval. The explanatory variables used in both models were species group (fixed factor, with seven levels for detection probability model like carnivores, big birds, horses, herons, small birds, medium-sized birds and wild boar and five levels for trigger speed. See details in Appendix S2), height (fixed factor, three levels: 30, 45 and 60 cm), camera trap model (fixed factor, five levels: BUS, KPG, LAC, RNY and SCT), sensitivity (fixed factor, three levels: low, moderate, high), period (fixed factor, two levels: day and night), sampling point (fixed factor, three levels), and distance interval (fixed factor, four levels, one every 2.5 m up to 10 m) at which the animal entered the FOV. With regard to the period, we considered night sequences to be those in which the IR flash was activated. In the probability of detection model, we also tested the interactions between height deployment and species group, camera trap model and species group, camera trap model and period, camera trap model and sensitivity, and height and distance interval. In the model for the trigger speed, we also tested the interaction between distance interval and species group. Since body size has been described as being one of the most important factors in camera trap detections (Hofmeester *et al.*, 2017), we followed Driessen *et al.* (2017) and pooled species of similar body size in groups for analytical purposes. Details on the grouping of species included are provided in Table 1, Appendix S2. The sequence was included in both models as a random effect factor and the sampling point (three levels) as a fixed factor (Harrison *et al.*, 2018). A backward stepwise procedure based on Akaike’s Information Criteria was applied to select the most parsimonious models (Akaike, 1974). *Post hoc* comparisons for categorical factors were performed using Tukey’s method. The models were validated according to the exploration of residuals and following to Zuur *et al.* (2010). The level of statistical signification was established at $P < 0.05$.

Results

The video camera recorded 3788 sequences of 27 different species, including reptiles, rodents, birds (including a high number of taxonomic families), lagomorphs, carnivores, and wild and domestic ungulates. The most frequent group was that of birds (2963 sequences), followed by mammals (819) and reptiles (4). The most frequently recorded species was the magpie (*Pica pica*), with 1923 sequences.

With regard to the camera traps, we recorded 270 530 photos that included 1083 independent sequences of animals that entered any FOV at a shorter distance than 10 m from the camera traps. We recorded 27 different species (see details in Appendix S2), and we did not discard any sequence due to

Figure 2 Box-plot of the average number of photos recorded per day by each camera trap model and sensitivity. Camera trap model abbreviations: BUS, Bushnell Trophy Cam Aggressor model 119774; KPG, KeepGuard 680V; LAC, Ltl Acorn Ltl-5310 Series; RNY, Reconyx HyperFire HC500; SCT, Scoutguard SG550BV.

problems to identify the species due to under- or over-exposed pictures. The minimum number of photos per day (including blank images) was obtained at low sensitivity. This pattern was consistent for all the camera trap models, but there were differences among them as regards the mean number of photos (Fig. 2).

With regard to the GLMM models, we discarded the groups of raptors, hare, deer, rodents and snakes from the analysis owing to the low sample size (i.e. number of sequences; see Appendix S2). When modelling trigger speed, we also discarded herons and small birds because of the low number of sequences of these groups detected by the camera traps. The best model for the probability of detection included the interactions between the camera trap model and period, the camera trap model and sensitivity, the camera trap model and species group, the species group and height and the distance interval and height (Table 2 and Appendix S3). The marginal coefficient of determination (R^2_m) calculated by theoretical method was 0.70. Detailed statistical results of this model are provided in Appendix S3.

In the case of the camera trap models, the probability of detection was significantly higher during the day than at night for all models, and significantly different for three of them (BUS, LAC and SCT; Fig. 3a; Appendix S3). We also found significant differences in the probability of detection as regards the sensitivity levels for all the models (a higher probability of detection was achieved at high sensitivity). In some models

(e.g. RNY), the predicted probability of detection differed as regards sensitivity levels, but in others (e.g. LAC and BUS), these differences were minimal. In summary, the highest probability of detection was obtained for BUS, which significantly differed from the other camera trap models, with the exception of LAC. The SCT achieved the lowest probability of detection, and was significantly different from BUS and LAC (Appendix S3). It should be noted that the time recorded and stamped by all the BUS devices ran progressively more and more slowly throughout the study period (Appendix S4). We noticed this during image processing, and corrected this time delay, as multiple camera traps were placed at the same point, and we therefore had multiple records of the same animals.

With regard to the species groups, the highest predicted probability of detection was obtained for wild boar and carnivores (>0.9), while the lowest was obtained for small and medium-sized birds (<0.4 , Fig. 3b-d; Appendix S3). Wild boar obtained a significantly higher predicted probability of detection than other species groups. Our results show that LAC achieved the highest probability of detection for all the bird groups, while BUS achieved the highest for carnivores and wild boar (Fig. 3b-d; Appendix S3). We also evidenced the relevance of camera trap deployment height, with significant effects on some species groups (e.g. herons), signifying that the maximum probability of detection was obtained at the minimum height deployment. With regard to the interaction between camera trap deployment height and distance interval, we found that, at shorter distances, the maximum probability of detection was obtained at a lower height, while as the distance between the animals and the camera traps increased, the highest probability of detection was obtained at higher heights.

Finally, in the case of the trigger speed, we obtained two best candidate models. The simplest one included species group, camera trap model, sampling point, distance interval and the interactions between species group and camera trap model, as well as species group and distance interval (Table 2 and Appendix S3). This model has an R^2_m of 0.26 and its statistical parameters are provided in Appendix S3. Upon considering the interaction between species group and distance interval, the closer the animal entered the FOV, the higher the probability of a fast activation (i.e. the animal was recorded in the distance interval at which it actually entered the FOV) for all the species groups, except the carnivores (Fig. 4). In the case of the carnivores, the expected probability of fast activation was close to 0.5 at all distance intervals. With regard to the interaction between species group and camera trap model,

Table 2 Candidate models explaining probability of detection and trigger speed, respectively

Candidate models	AIC	Response variable
SpG + Hei + CTM + Sen + Per + Poi + Int + SpG*Hei + SpG*CTM + CTM*Per + CTM*Sen + Int*Hei	9867.7	Probability of detection
SpG + CTM + Poi + Int + CTM*SpG + SpG*Int	2978.0	Trigger speed
SpG + CTM + Poi + Int + Hei + CTM*SpG + SpG*Int	2979.4	Trigger speed

All models include ID sequence as a random effect factor.

Abbreviations: CTM, camera trap model; Hei, camera trap deployment height; Int, distance interval; Per, period; Poi, sampling point; Sen, sensitivity; SpG, species group.

Figure 3 Predicted values for probability of detection of the GLMM model (see Table 2) regarding the interactions between (a) period and camera trap model, (b) species group and camera trap model, (c) height deployment and distance interval of detection, (d) height deployment and species group and (e) sensitivity and camera trap model. Camera trap model abbreviations: BUS, Bushnell Trophy Cam Aggressor; KPG, KeepGuard 680V; LAC, Ltl Acorn Ltl-5310 Series; RNY, Reconyx HyperFire HC500; SCT, Scoutguard SG550BV. Species group abbreviations: CA, carnivores; BB, big birds; HO, horses; HE, herons; SB, small birds; MB, medium birds; WB, wild boars. Error bars are standard errors.

big birds obtained the highest probability of fast activation, and carnivores the lowest for all the models; but there were differences among the models as regards horses, medium-sized birds and wild boar (Fig. 4a).

Discussion

In this study, we tested five models of some of the most frequently used makes of camera trap to include a range of

Figure 4 Predicted values for the trigger speed GLMM model (Table 2) in relation to the interactions between (a) species group and distance interval and (b) species group and camera trap model. The probability of fast activation represents the probability of recording an animal at the distance interval in which it actually entered the field of view of the camera trap. Camera trap model abbreviations: BUS, Bushnell Trophy Cam Aggressor; KPG, KeepGuard 680V; LAC, Ltl Acorn Ltl-5310 Series; RNY, Reconyx HyperFire HC500; SCT, Scoutguard SG550BV. Species group abbreviations: CA, carnivores; BB, big birds; HO, horses; HE, herons; SB, small birds; MB, medium birds; WB, wild boars. Error bars are standard errors.

models and features that are indicative of what is on the market (there are dozens of models and several for each make). We demonstrated that false-negatives can lead to substantial data loss, and we identified the main factors that influence the probability of detection (i.e. the probability of the camera successfully capturing a usable photograph of an animal passing through the FOV) and trigger speed (i.e. the time delay between the instant at which a motion is detected, and the time at which the picture is taken) of each one under our study conditions. Overall, our results provide empirical guidelines for best practices in camera trapping research, thus enhancing the applicability, robustness and reliability of camera trapping studies (Fig. 5).

It is frequently stated that false triggers (i.e. blank images) drain battery life and fill memory card space, in addition to increasing the amount of time required for image processing (Rovero & Zimmermann, 2016). Some authors have pointed out that higher and angled placements, along with higher temperatures, generate more blank images (Jacobs & Ausband, 2018). Our results confirm that the number of blank images is higher when the sensitivity of the camera traps is higher (Fig. 2; Welbourne *et al.*, 2016). However, to the best of our knowledge, there are no previous studies evaluating this relationship. Some studies have found a correlation between the number of detections of animals and the number of blanks (Driessen *et al.*, 2017). In this study, we have obtained the

highest probability of detection with high sensitivity for all the camera traps tested, with the exception of KPG (Fig. 4e). These results can be explained by the fact that at high sensitivity, camera traps are constantly activated by vegetation (or other variables), and the probability of ‘randomly’ recording animals is, therefore, higher; but this constrains the life of the batteries and memories. Although a high probability of detection is always desired, high sensitivity will suppose a trade-off between detection and memory and battery limitations (Fig. 5). In this respect, the hot and dry scenario in which the study was carried out should be highlighted, which could influence the performance of the cameras.

We also found a significant interaction between the period of the day and the camera trap model with which to explain the probability of detection (Fig. 3a). This probability was lower at night than during the day, which is consistent with the previous studies (Rowcliffe *et al.*, 2014). The magnitude of differences varied among models. Broadly, this is highly relevant for camera trapping studies based on encounter rates (Mills *et al.*, 2020) and those focused on activity patterns (i.e. proportion of the day that animals spend moving), key parameters with which to estimate population density (Palencia *et al.*, 2021a), species interactions (Niedballa *et al.*, 2019) or even when they are the target parameter themselves (Distiller *et al.*, 2020; Edwards *et al.*, 2020). We conclude that the effect of the period of the day should be considered when analysing camera

Key factors	Practical limitations	Practical recommendations
Sensitivity	Trade-off between detection sensitivity and memory and battery capacities because of blank-images	Set high sensitivity only when memory and battery can be checked frequently, and/or when open areas are sampled
Day time	Different probability of detection between day and night time	Include this variability in the models when analysing daily parameters (e.g. activity)
Models	Different probability of detection according to models (makes)	Avoid using different camera trap models in the same study
Height	Bias in probability of detection when camera traps are not set at shoulder height of target species	Monitor exclusively morphologically similar species, consider specific sampling design for each species, or place more than one camera at different heights
Trigger speed	Slower activations as more distant animals enters FOV	Use lure to increase the amount of time in front of the FOV (if it does not violate method assumptions)

Figure 5 Limitations and recommendations obtained in this study as regards key camera trapping factors. This could be considered as best-practice guide when working with camera traps. Abbreviations: FOV, field of view (area captured by a camera trap).

trapping data to avoid biased results (Fig. 5) by, for instance, weighting the encounter rates (Rowcliffe *et al.*, 2014).

As has occurred in previous studies, we found that the probability of detection varied among camera trap models (Fig. 3). Camera traps are sometimes classified as ‘recreational’ (e.g. Bushnell TrophyCam) *versus* ‘professional’ (e.g. Reconyx Hyperfire PC800) on the basis of technical specifications and price (Newey *et al.*, 2015). However, upon considering the results reported both here and in previous studies (Apps & McNutt, 2018), these categories do not always correspond to performance. Some cheaper camera trap models can perform just as well as or even better than more expensive ones (Driessen *et al.*, 2017). In this respect, the published studies are not consistent. For instance, some studies have indicated the poor performance of Reconyx when compared with Little Acorn and Bushnell (Apps & McNutt, 2018; Fancourt *et al.*, 2018; Seccombe, 2017; Urbanek *et al.*, 2019), or even the variability in Reconyx devices (Heiniger & Gillespie, 2018). Other studies have reported a higher performance for Reconyx and Bushnell cameras (Swann *et al.*, 2004; Wellington *et al.*, 2014; Yajima

& Nakashima, 2021). This inconsistency found in the bibliography could be explained, at least partly, by the target species. Our results showed a significant interaction between camera trap model and species group. The LAC cameras achieved the highest probability of detection for all bird groups, which can be explained by the two levels of Fresnel detection window (Welbourne *et al.*, 2016) that cover a wide range of heights. For those makes with only one horizontal detection band (e.g. RNY), the performance may be lower when detecting small animals (e.g. birds) close to the cameras if the cameras are angled parallel to the slope ground. In the case of SCT camera traps, our results are consistent with those reported in most of the published studies in which Scoutguard models are shown to have a low performance (Driessen *et al.*, 2017; Seccombe, 2017; Swann *et al.*, 2004). In this respect, a relevant problem will emerge in the coming years in those camera trapping long-term studies in which newer cameras usually replace the old (stolen or broken) ones. Overall, our recommendation is to avoid using different camera trap models (and even different models of the same make) in the same study (Fig. 5) or

considering camera trap model as covariate in the analysis. Additionally, the malfunction observed on Bushnell clock could be a relevant issue for most of camera trap studies in which only one camera is placed per site. This issue should be checked under controlled scenarios since the correction is non-trivial.

The influence of camera trap deployment height on the probability of detection is inconclusive, with some studies suggesting no influence (Jacobs & Ausband, 2018), lower detection rates for higher deployments (Meek *et al.*, 2016), that small variations in height can result in missed photos (Swann *et al.*, 2004), or that camera traps should be mounted at the target animals' shoulder height (Apps & McNutt, 2018; Meek *et al.*, 2014). The significant interaction between camera trap deployment height and species group obtained here can be explained by considering the different heights of the species analysed. We set the camera traps at shoulder height for carnivores, big birds, herons and wild boar (Figs. 1–3d). However, all the camera traps were below the horses' shoulders, and above those of small and medium-sized birds, which are the three species groups that achieved the lowest probabilities of detection. These results are particularly relevant for studies that consider more than one target species, such as those focused on estimating species inventories (Tobler *et al.*, 2008) and/or interspecific interactions (Niedballa *et al.*, 2019; Triguero-Ocaña *et al.*, 2020). In spite of the fact that camera trapping is usually considered as a multispecies approach (Rovero & Zimmermann, 2016), the number of detections may be biased (underestimated) for all species for which the camera traps are not set at shoulder height. We recommend multispecies studies using camera trapping exclusively to monitor morphologically similar species or considering a specific sampling design for each species (e.g. placing several camera traps at different heights).

The significant interaction between camera trap deployment height and distance interval suggests that lower deployments increase the probabilities of detection at closer distances, while higher probabilities of detection at further distances are achieved at higher deployments. This result can be explained by the fact that a lower height reduces the chance of small animals passing beneath the camera trap PIR zones at a short distance, but will also reduce the range of distances over which animals can be detected, since vegetation may obstruct the PIR zones (Howe *et al.*, 2017). Furthermore, higher deployments reduce the obstruction of herbaceous vegetation in the PIR zone but increase the probability of small animals passing beneath the PIR zones. We recommend defining the deployment height on the basis of the target species and considering the removal of herbaceous vegetation when small species are the target (Fig. 5). This recommendation is particularly relevant for certain analytical camera trapping methods that assume certain detection close to the camera (Howe *et al.*, 2017).

With regard to the model for trigger speed, we found a strong negative relationship with distance (the closer the animals that entered were to the camera traps, the greater the probability of rapid activation), with the exception of carnivores (Fig. 4a). This may be a consequence of a decrease in

PIR sensitivity as the distance between the animal and the camera trap increases. This decrease is highly noticeable, bearing in mind that for a given speed, the time that the animal spent crossing from one side of the FOV to the other was considerably shorter at the first interval (i.e. from 0 to 2.5 m from the camera; narrow, and area around 3 m²) when compared to the last one (i.e., from 7.5 to 10 m from the camera; width, and area around 20 m²). This result is relevant for camera trapping methods when a specific and rapid detection in the centre of the FOV is assumed (Nakashima *et al.*, 2018), since this should take place only very close to the camera trap (Hofmeester *et al.*, 2017). In the case of carnivores, we suspect that their rapid movement could mask the decrease in PIR sensitivity with distance (Palencia *et al.*, 2021b). With regard to birds, we obtained a significantly higher probability of rapid activation for big than for medium-sized ones, which can be explained by differences in their movement behaviour. While big birds (mostly storks) usually made very slow movements, medium-sized birds (mostly magpies) usually made short flights and nervous movements, thus implying that individuals constantly transited between different distance intervals. In this respect, relatively fast-moving species, such as foxes and magpies require a faster trigger speed than slower species. When carnivores are the target species, and depending on the aim of the study, we recommend using lures to increase the amount of time that animals spend in front of the camera if this does not violate method assumptions. It should be noted that despite the significant effect of the camera trap model, we did not find any association between theoretical trigger speed (ranging from 0.25 to 1.2, Table 1) and the probability of rapid activation. This can be explained as a consequence of the variability in intra-camera trigger times observed in other studies (<https://www.trailcampro.com/collections/trail-camera-reviews>; Palencia, Rowcliffe *et al.*, 2021), the type of detection zone (zonal or conical, Driessen *et al.*, 2017), and the relatively wide intervals (width = 2.5 m) that have been considered here to evaluate the trigger speed. Future studies therefore should be designed to explore the relevance of the trigger speed by considering shorter intervals, and potentially, not only radials but also angled intervals (Howe *et al.*, 2017; Rowcliffe *et al.*, 2011).

In conclusion, we have described the key factors to consider when working with camera traps, since they determine the performance of cameras. The results reported here provide empirical guidelines for best practices as regards choice of camera trap, set up and study design (Fig. 5), and highlight the high variability of camera trap performance as a consequence of a wide range of factors. Researchers should, therefore, consider the parameters and capabilities of camera traps very carefully in study designs and data analysis, otherwise results may be biased. Moreover, it is highly beneficial for researchers to be aware of the range of cameras available and their relative advantages before investment and use. Empirical experiments, such as those carried out in this study, enhance the applicability, robustness and reliability of camera trapping studies when used to monitor wildlife populations. It will be necessary to constantly re-evaluate the performance of camera traps given the rate at which they continue to evolve.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Video clip of a red deer entering the field of view of the camera traps.

Appendix S2. Species grouping details.

Appendix S3. Tables showing best models for probability of detection and trigger speed.

Appendix S4. Time delay observed for Bushnell camera traps.