



Research Article

“Which camera trap type and how many do I need?” A review of camera features and study designs for a range of wildlife research applications

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Abstract

Automatically triggered cameras taking photographs or videos of passing animals (camera traps) have emerged over the last decade as one of the most powerful tool for wildlife research. In parallel, a wealth of camera trap systems and models has become commercially available, a phenomenon mainly driven by the increased use of camera traps by sport hunters. This has raised the need for developing criteria to choose the suitable camera trap model in relation to a range of factors, primarily the study aim, but also target species, habitat, trapping site, climate and any other aspect that affects camera performance. There is also fragmented information on the fundamentals of sampling designs that deploy camera trapping, such as number of sampling sites, spatial arrangement and sampling duration. In this review, we describe the relevant technological features of camera traps and propose a set of the key ones to be evaluated when choosing camera models. These features are camera specifications such as trigger speed, sensor sensitivity, detection zone, flash type and flash intensity, power autonomy, and related specifications. We then outline sampling design and camera features for the implementation of major camera trapping applications, specifically: (1) faunal inventories, (2) occupancy studies, (3) density estimation through Capture-Mark-Recapture and (4) density estimation through the Random Encounter Model. We also review a range of currently available models and stress the need for standardized testing of camera models that should be frequently updated and widely distributed. Finally we summarize the “ultimate camera trap”, as desired by wildlife biologists, and the current technological limitations of camera traps in relation to their potential for a number of emerging applications.

Camera trapping is the use of remotely triggered cameras that automatically take images and/or videos of animals or other subjects passing in front of them (Fig. 1). This tool is widely used across the globe especially to study medium-to-large terrestrial mammals and birds (reviews in Rovero et al. 2010; O'Connell et al. 2011; Meek et al. 2012a), arboreal mammals (e.g. Goldingay et al. 2011), small mammals (e.g. Oliveira-Santos et al. 2008) and herpetofauna (e.g. Pagnucco et al. 2011). Over the last 10 years, and in particular since 2006, there has been a substantial growth in the number of published camera trap studies (Rowcliffe and Carbone 2008; McCallum 2013; Fig. 2). Even though camera trapping has been used in ecological studies for decades (Kucera and Barrett, 2011), its application expanded with the advent of commercial wildlife camera traps in the early 1990s and, more recently, with the advent of digital camera traps.

The most common camera trapping research applications include (1) faunal checklists and detection of elusive or endangered species (e.g. Sanderson and Trolle 2005; Rovero and De Luca 2007; Tobler et al. 2008), (2) relative abundance estimation by using camera trapping photographic rate (Carbone et al., 2001; O'Brien et al., 2003; Rovero and Marshall, 2009), (3) abundance and density, survival and recruitment estimations of individually recognizable species through Capture-Mark-Recapture analysis (Karanth and Nichols, 1998; Karanth et al., 2006), (4) density estimation of non-recognizable species through the Random Encounter Model proposed by Rowcliffe et al. (2008), (5) oc-

cupancy estimation and modelling (Linkie et al., 2007), (6) monitoring populations and communities over time (O'Brien et al., 2010; TEAM Network, 2011), (7) analysis of habitat associations (Linkie et al., 2007; Bowkett et al., 2008; Bater et al., 2011), and (8) a range of species-specific or focal purpose studies on activity patterns (Tobler et al., 2009; Meek et al., 2012b), diet (e.g. owls; Juillard 1987), reproduction (e.g. juvenile lynx, wolf packs), behaviour e.g. detecting marking sites (Vogt et al., in review), monitoring kill sites for Eurasian lynx (Zimmermann et al., 2011), identification of livestock raiders or carcass consumers (Bauer et al., 2005), disease monitoring (Borchard et al., 2012), detection of individuals with abnormal phenotypic characteristics, such as in wolves (Berzi et al., 2010), monitoring of wildlife crossings or green bridges (Clevenger et al., 2009).

This wide range of research applications has been accompanied by a vast diffusion of commercial camera traps, a phenomenon which however has been driven mainly by the demand of hunters using this tool to detect their targets. In turn, this has raised the need for knowledge related to both the choice of suitable models and the sampling design to conduct scientifically valid research (Kays and Slauson, 2008; Swann et al., 2011). With this review, we build on the literature and our own experience and we aim to (1) describing the relevant technological features of camera traps and proposing a set of key features upon which selecting camera traps, and (2) reviewing key research applications in terms of camera trap performance requirements and sampling design. We therefore hope to aid ecologists and managers who plan to use camera traps in deciding which types of systems and features are most appropriate for their particular study.

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Figure 1 – Collage of camera trap images from around the world. Top left: Eurasian lynx, *Lynx lynx*, moving in snow in Switzerland and monitored with camera traps by KORA (photo by KORA). Top right: a rare documentation of a wolf, *Canis lupus*, camera trapped in central Italy, with signs of hybridization with dog and bearing an iron snare on its neck (photo by D. Berzi). Bottom left: Abbott's duiker, *Cephalophus spadix*, a rare and threatened forest ungulate in Africa, endemic to a few sites Tanzania, whose first ever images in the wild were taken with camera traps (photo by F. Rovero). Bottom right: red necked pademelon, *Thylogale thetis*, a shy and forest-dwelling marsupial living in the eastern coastal region of Australia (photo by P. Meek).

How do camera traps work?

Camera trap functioning is complex and has changed vastly from early models (Shiras, 1906, 1913; Guiler, 1985) to current day models. The first, commercially available camera traps in the 1980s were Xenon white flash systems with circuitry separate to the camera, which was often an off-the-shelf camera wired to respond to a break in an infrared beam [Active Infra-red (AIR), see below]. These systems required the camera trap and the triggering devices to be separate to one another, and required the infrared beam to be broken by an animal passing through the beam thus triggering the camera to take a photo. Over the last 20 years, technological advances have led to sophisticated inbuilt units made by a self-contained package including sensors and camera.

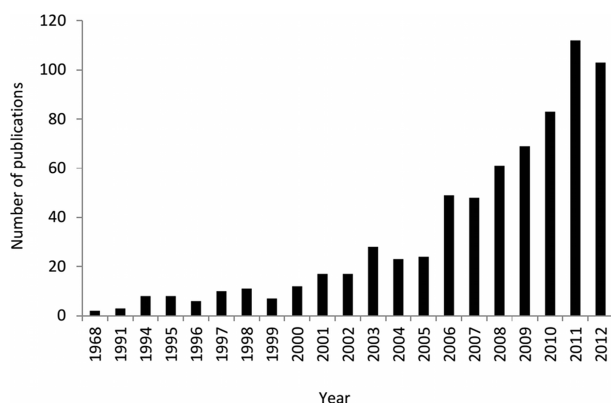


Figure 2 – The number of camera trap papers published per year standardized by the total number of papers published (relative frequency expressed per 1000; sample sizes are 692 camera trapping papers and 656566 total papers) according to the Web of Science's categories ecology, biology, zoology and veterinary sciences queried for terms "camera trap", "infrared triggered camera", "trail camera", "automatic camera", "photo trap", "remotely triggered camera", "remote camera".

The majority of modern day camera traps rely on a passive infrared sensor (PIR) to detect a differential in heat-and-motion between a subject and the background temperature, and on an infrared/LED flash array to illuminate the target area. All animals have a heat signature in the infrared spectrum and the PIR detects this difference and triggers the camera (Meek et al., 2012a). For a comprehensive glossary of technical terms we refer to Meek et al. (2012a).

The range of camera trap brands and models currently on the market is vast, with new functions being developed each year. Camera brands and models can vary greatly in features and specifications (Cutler and Swann, 1999; Swann et al., 2011), however they have consistent features and components to function, the main ones being shown in Figure 3. Here, we first describe the fundamental technological features that determine the type of camera trap system.

Passive Infra-red (PIR) sensor: the passive detector of heat-in-motion, called pyroelectric sensor. A limitation of PIR sensors is the way they detect differences between the target animal and the background temperature. Optimum condition for camera trapping is where the temperature differential between the target and the background is greater than 2.7° C (see Meek et al. 2012a). Hence, when ambient temperature falls within the body temperature range of most mammals (31.5–36.5° C, with recorded peaks of 42.5° C), PIR camera traps can be unreliable. A second limitation of PIR sensors is that they can be triggered by the movement of pockets of hot air or by the motion of vegetation in the detection zone. This problem can be limited by avoiding to point the camera directly to background that is under sun incidence.

Detection Zone: the area in which a camera trap is able to detect the target through its sensor. The detection zone is not necessarily equal to the camera field of view, i.e. the area included in the actual photograph. Detection zones vary between camera trap models (details below), and for some, only a small proportion of the field of view actually corresponds to the camera's detection zone. Some models sense through a

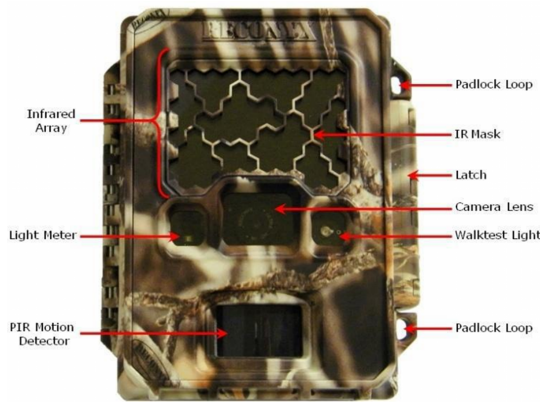


Figure 3 – Diagram of a Reconyx HC600 depicting the main components of a camera trap (Copyright Reconyx Inc.).

conical shaped detection zone while others through a combination of horizontal bands and vertical axis zones, depending on the technical specifications of the PIR sensor.

Trigger speed (or “trigger delay”): the rapidity with which the camera captures an image relative to when the sensor detects the passing target. A “fast” trigger speed (usually < 1 s) increases the probability of a target being recorded; a “slow” trigger speed may result in missing targets. This feature should be more correctly called “trigger delay”, with low delays corresponding to fast trigger speed, however we retain the name “trigger speed” because of its common use. Trigger speed and detection zones are interacting parameters, because a slow trigger speed can be compensated for by a wide detection zone.

Based on both sensor and flash technology, there are three main categories of camera traps:

1. PIR with infrared flash: the majority of camera traps on the market today use PIR, despite the aforementioned shortcomings, coupled to an infrared LED flash, taking monochrome images at night.

2. PIR with white flash: two types of white flash cameras are available on the market despite a considerable downturn in the demand for these camera traps (Meek and Pittet, 2012): Xenon and white LED. Xenon gas based flash systems were amongst some of the earliest of camera trap designs but faded into the background once infra red technology was used in the devices. In recent times however, the demand for white flash camera traps has been re-ignited and, in 2012, two Reconyx and Scoutguard models mounting white LED flashes were released on the market. However, the performance of white LED flashes does not match the Xenon gas flashes when optimal picture clarity is required (see below).

3. Active infrared (AIR) with infrared flash: these systems are not widely used in recent times although at a recent colloquium their wide application and advantages over PIR were reiterated (Meek et al., in preparation) and steps have been taken to rekindle this form of triggering system. Faunatech Australia is one of the few remaining companies that still market this type of camera trap.

In addition, a limited number of PIR camera trap models (e.g. Spy-point, Bolymedia) have dual flashes (Xenon and infrared flash). With this option the user can choose the optimal flash according to the study aim.

Camera features for choosing models

A clear vision of the research question and hence the adequate sampling design must precede the choice of camera trap features (see Nichols et al. 2011). A number of practical and local environmental factors will also affect the choice on best camera type, notably target species, site accessibility, climate, target site (if trails or focal points such as water ponds or baited stations), habitat (open vs. densely covered in vegetation). This is because the various camera trap features will result in varying performance depending on these factors. For example, sensitivity will perform differently according to body size of the tar-

get species and to local temperature; flash intensity will affect results depending on target site (e.g. a narrow trail or a wider zone) and animal size; camera dimensions and casing will be especially useful for remote and/or extreme weather sites; power autonomy will be relevant for studies where cameras cannot be regularly checked.

We propose the following 10 camera features be evaluated when choosing camera trap type and models. We do not explicitly consider camera cost here, although it is one of the most influential factors when researchers choose a camera model (Meek and Pittet, 2012). However cost is mainly a function of camera performance, as for example, cameras that are resilient in tropical climate with fast trigger speed, weather-resistant case and high quality images will likely cost more than less robust cameras with slow trigger speed.

1. Trigger speed: this is a fundamental feature of cameras, if not the critical one. Fast trigger speeds may be less necessary if the target is being attracted to a feeding station, a carcass or a lure.

2. Flash type (white or infrared): cameras with white flash are fundamental when sharp and colour pictures are needed at night as well as in day time, as is the case of Capture-Mark-Recapture (CMR) studies that require individual recognition (see below), or for faunal inventories, as colour pictures will increase chances of identifying species. Currently, classic Xenon flashes outperform white LED flashes in terms of image sharpness, because the Xenon flash is more powerful and the flash duration is short enough (order of 10^{-3} s) to freeze moving animals. Recently moreover, no-glow (also called “black”) IR flashes have been introduced to minimize the red glow emitted by standard IR LEDs which is seen by animals (P. Meek and KORA, unpublished data). These no-glow flashes should minimize trap-shyness by animals and limit risk of damage or theft by humans. However, while no-glow flash may be invisible for humans, there is evidence that they are still seen by animals; moreover, cameras are heard by animals, possibly because they emit noise in the ultrasonic range (P. Meek and KORA, unpublished data).

3. Detection zone: this is a critical, albeit overlooked feature. Detection zone area varies widely among current models (15.8–324.1 m², data in Meek et al. 2012a). Cameras with a narrow detection zone, i.e. smaller than the camera field of view, have usually fast trigger speeds and will take the photo when the animal is well within the field of view. The detection zone can be increased to some extent by moving the camera further away from the target, which can compensate for slow trigger speeds.

4. Number of photos taken, recovery time, and video: a number of infrared-flash cameras are capable to take bursts of images in rapid sequence (i.e. fast recovery time), which may be important for a number of purposes: better animal identification (as chances of obtaining a good image within a burst will be increased, especially when animals are not moving too fast), recording individuals within family groups and packs, analysis of passing sequences to derive day range which is a critical parameter in the Random Encounter Model (REM; Rowcliffe et al. 2008). At night, Xenon gas white-flash cameras are not capable to take photo bursts or videos due to the recharge time of flash that can take ≥ 30 s. This limitation is overcome by recently proposed white-LED flash cameras. Rapid image sequences and real videos can be useful for behavioural studies or specific research needs (e.g. in north-eastern Italy, videos are used to study the use of rubber tress by brown bears; F. Rovero, unpublished data). However data handling is more time consuming, memory cards are saturated faster and power consumption is greater, hence videos are not recommended when photographs alone provide the data required.

5. Sensitivity: a setting, often adjustable, that regulates the sensor responsiveness to the target by changing the heat sensitivity threshold. In general, high sensitivity is better to detect small-sized animals, however high sensitivity will increase chance of misfiring when sun hits the target site and is more likely to be triggered by moving vegetation.

6. Flash intensity: a number of digital camera models allow to adjust flash intensity automatically to the distance of the subject from the camera. Some models enable to adjust the amount of light generated by the white flash for two to three distance settings (e.g. UWay UV532)

while in the majority of models the flash is programmed for maximum distance and illumination. The Cuddeback Attack has a setting that adjusts the ISO hence adjusting the image sensor sensitivity to light. The Reconyx PC850 and HC550 adjust intensity according to the distance an animal is from the device. The newly released Scoutguard 860C uses white LED illumination and using a firmware upgrade can be adjusted for close settings.

7. *Power autonomy*: studies in remote areas or deploying intense sampling often require high power autonomy; generally, cameras with white flash consume more battery power than infrared flash. The three most common battery types used by camera traps are Lithium, Nickel-Metal Hydride (NiMH) and Alkaline. Lithium batteries are the most preferred type of battery for their high-power output and resilience, but are also the most expensive and only have one life, unlike rechargeable batteries. Nickel-Metal Hydride (NiMH), or rechargeable batteries, are advantageous over Alkaline and Lithium batteries in that they allow multiple-uses. Importantly moreover, they produce less toxic waste in landfill, and can be recycled. However, all rechargeable batteries are lower voltage than Alkaline and Lithium batteries and so reduce camera trap run time and might alter camera trap performance. Alkaline batteries are the most common battery type and they are widely used in camera traps although they discharge quicker than NiMH and Lithium. A number of camera models (e.g. Spypoint, Bolymedia, Uway) mount an input jack for external batteries or small solar panels, thus higher capacity, lead-acid batteries can be used to prolong deployment. Despite the higher initial costs, we highly recommend using rechargeable batteries as long as camera-trap performances are not altered. Most modern camera traps currently use batteries of AA size.

8. *Image resolution, sharpness and clarity*: the majority of camera traps on the market take medium-to-high resolution pictures and videos, however a more critical feature is the sharpness and clarity of colour images, needed for individual identification and in some cases to identify species. For night pictures, only those taken with a white Xenon flash are clear and sharp enough to allow individuals identification of naturally marked species. Moreover, the resolution and clarity of images is often critical when using camera traps for small animals, especially where sympatric species coexist and morphological features can be similar. However, we warn that the number of pixels declared in camera trap specifications is often larger than real due to pixel in-

terpolation. In addition, the increase in pixel number is often accompanied by an increase in digital noise and chromatic aberrations. On the other hand, the higher the (true) image resolution, the slower the shutter speed, which can determine blurred images; therefore, a compromise between resolution and shutter speed is needed to produce the sharpest images.

9. *Camera housing and sealing*: the housing, camouflage and water and insect proof qualities of camera traps is extremely important in wildlife research (Swann et al., 2011; Meek and Pittet, 2012). This is especially so where extreme weather conditions are experienced (snow, rainfall and humidity). The weight and size of the camera trap can also be important in many contexts. In addition, ability to protect cameras with metal cases and lock them is critical against theft and/or damage by large animals. Housing should allow easy attachment of the unit to the tree or support used, including replacing batteries and memory cards without need to move the camera from its support. Cameras should ideally have a tripod stud on the rear and underside of the housing for attaching the positioning brackets (Meek and Pittet, 2012).

10. *Camera programming and setting*: these should be as simple as possible, to allow for field workers with varying degree of experience to set camera traps without errors. In addition, most cameras have the option of programming the operation time, to avoid unnecessary images, which may be useful for example when only nocturnal species are targeted.

Camera performance and study designs

It is beyond the scope of this review to address all study designs that deploy camera trapping, however we focus on the following four major research designs, and detail particularly the aspects that are relevant to choosing camera type, namely number of camera sites, camera days, placement design and camera features (Tab. 1): (1) general faunal detection and systematic inventories of terrestrial mammals and birds; (2) occupancy studies; (3) density estimation through CMR; (4) density estimation through REM.

1. Faunal detection and inventories

To conduct a general faunal inventory by camera trapping, one needs to maximize the chances of capturing clear images of the greatest number

Table 1 – Summary of sampling designs and camera features for key study types that deploy camera trapping.

Study type	Number of camera sites	Camera-days	Placement	Camera features
First assessment, inventory	Variable	1000-2000 for tropical communities	No requirements, maximise captures, ensure key habitat represented, baiting can be done if inventory is the only aim	White flash, high sensitivity if small species are targeted, large detection zone, fast trigger speed
Occupancy	> 60, but depending on detection probability (p) of target species	Enough to reach sufficient p for target species (TEAM Network 2011 uses 1800)	Regular grid, spacing depending on species with larger home ranges, more sites will ensure more species with $p > 0.1-0.2$	IR flash, sensitivity tuned to species size
Density estimation through Capture Mark Recapture (CMR)	Trade-off between trap density and size of the sampled areas: 10-30 individuals exposed with a trap sites density of at least 2-4 per smallest home range	As short as possible to assume demographic closure but long enough to have enough recaptures (>60)	Sampled areas maximising the area-to-perimeter ratio, 2 camera traps at each site, for carnivores optimal placements along trails	Xenon white flash with different distance settings, short delay between consecutive pictures, high sensitivity if small target species, fast trigger speed, either two Xenon white flash camera traps per site or one Xenon white flash combined with an IR or white LED camera trap which allows bursts of photos per trigger
Random Encounter Model (REM)	> 50	Depending on target species, enough to obtain 50 independent events	Random relative to animal movement, grid preferred, avoid multiple captures of same individual, area coverage important for abundance estimation	IR flash, high sensitivity if small species are targeted, fast trigger speed, bursts of photos

of species possible. Accordingly, the ideal camera should have high sensitivity, fast trigger speed, wide detection zone (especially if trigger speed is low), and appropriate power autonomy to be left for relatively long time (minimum 30 days). Critically, white flash cameras (particularly those mounting Xenon flash whose images are sharper than those of white LED flash) will be better to obtain colour pictures at night and day and hence facilitate identification. In tropical countries, cameras will need to be robust and resistant to moisture, rain and insect intrusion.

In terms of sampling design, single camera traps should be set throughout the study areas. Camera placement can be opportunistic, hence cameras can be placed along intensively used wildlife trails, nests, feeding or drinking sites. Cameras can also be baited, unless the data are also meant for rigorous statistical analysis, such as occupancy (see below). The attractant may optimize the chance of luring a passing animal into the detection zone. The spatial arrangement of camera traps for this study design is also flexible. There are no strict requirements on minimum distances between camera traps or total survey area to be covered. Tobler et al. (2008) indicated that the area covered by the camera traps may have little impact on the number of species detected; inventories may therefore be conducted in a sampling area that is representative of the total study area and main habitat types (e.g. dense forest, woodland, wooded grassland, grassland, etc.). However, the even spacing of camera traps in grids allows for more rigorous statistical analysis including occupancy analysis and is generally recommended for monitoring purposes (see below).

The completeness of sampling effort in terms of species recorded can be assessed by building species accumulation curves and looking at the levelling off; estimators can be used to estimate the total number of species (see Tobler et al. 2008 for an example). Software PRESENCE (Hines, 2006) and GENPRES (Bailey et al., 2007) provide simulation facilities to determine the required sample size for a desired level of precision in species richness. Survey effort is usually measured in camera trap days, which is the number of camera traps multiplied by the number of days they operated. In many areas, especially tropical countries that hold very diverse communities of terrestrial vertebrates, many thousand camera trap days are required to obtain a fairly complete species list (Srbek-Araujo and Garcia, 2005; Azlan, 2006; Tobler et al., 2008); however, there is firm evidence that 1000 to 2000 camera trap days may be enough for detecting 60-70% of the species (Tobler et al. 2008; Ahumada et al. 2011; F. Rovero, unpublished data). The time needed to carry out a survey is inversely proportional to the number of camera traps used. Hence, the larger the number of cameras deployed, the quicker the adequate effort will be reached.

Unlike surveys designed for CMR analysis, where the survey period must be limited to a few months to guarantee population closure (see below), there is no time limit for camera trap inventories, as it can be often assumed that the diversity of most species does not change over a period of a year. Researchers can therefore run a small number of camera traps over many months, or surveys can be spread out over multiple shorter periods throughout a year. When using a small number of camera traps we recommend moving camera traps every 15 to 30 days, if feasible, to avoid bias caused by the camera trap locations and to sample a large enough area.

While these indications apply to general inventories of medium-to-large species, focal species – or groups of species – detection will need specific camera features and designs. For example, if one targets small-bodied species, camera sensitivity will become critical. Likewise, when animal's coat colour and pattern is of relevance (e.g. assessing skin diseases, detecting suspected new species or range records, recording poaching signs on animals, etc.), then obtaining sharp high quality colour pictures will be critical; for example, the obtainment of colour pictures was instrumental to identify a new species of giant sengi, or elephant-shrew, from Tanzania (Rovero and Rathbun, 2006).

2. Occupancy studies

Occupancy is defined as the proportion of area, patches or sites occupied by a species (MacKenzie et al., 2002, 2006). These authors de-

veloped a model to estimate site occupancy and detection probability based on repeated presence-absence surveys of multiple sites. Hence, true occupancy estimation accounts for the state variable “present but not detected” (detection probability $p < 1$) in addition to “present” and “absent” only (i.e. naïve occupancy). The basic sampling scheme implies multiple visits to a randomly selected set of sites within a short interval of time so that sites are closed to changes in occupancy states (O’Connell and Bailey, 2011). Occupancy analysis is well suited to camera trapping data, because detection data can be collected over a greater number of sampling occasions than through other methods such as counts of signs or sightings. Occupancy can be used as a surrogate for abundance especially for species with relatively small ($< 5\text{--}10\text{ km}^2$), well defined home-ranges so that a large enough area can be sampled simultaneously by camera traps. In this case, one can assume that each individual can only appear in one camera trap, and the camera trap grid should cover a representative portion of the population. If home-ranges are large in comparison to camera trap spacing then one single individual can appear in many different camera traps and there will be little correlation between occupancy and abundance.

Cameras with fast trigger speed will be critical not to miss detection of passing animals. Other requirements, such as sensitivity, will depend on target species. Cameras should be set out in a regular grid with approximately equal distances between cameras. Camera placement at the identified site in the grid should ideally be passive and random, i.e. it should not favour particular locations such as feeding or drinking sites where animal abundance may be higher than average. Cameras should cover all habitat types of interest and the number of camera traps in each habitat type should be proportional to habitat extent (i.e. stratified sampling design) and sufficiently large to allow for statistical analysis. If possible the distance between camera traps should be larger than the diameter of the average home range of the species of interest, to avoid spatial auto-correlation. If the home range diameter of a species is much larger than the distance between camera traps the results should be interpreted as the percentage of area used by a species during the survey period instead of the percentage of an area occupied (MacKenzie and Nichols, 2004). When multiple species are targeted, camera spacing will need to be spread out enough so that larger species with larger home range can be sampled with sufficient detection probability without over-spacing, as this may result in missing species with smaller home range. TEAM Network (2011) designed a protocol to sample the communities of medium-to-large terrestrial vertebrates in tropical forests by spacing camera points in a grid of 1 camera every 2 km^2 .

The survey time needed largely depends on the detection probabilities of the species of interest. The higher the detection probability, the fewer survey days are needed to collect reliable data. Single-season occupancy models assume that occupancy does not change over the survey period and surveys should therefore be limited to a maximum of two to three months. If species are known to seasonally migrate in and out of the study area surveys should be conducted outside the migration period. Generally, occupancy studies require a large number of camera traps to produce reliable data, especially when assessing changes in occupancy over time (e.g. TEAM Network protocol adopts 60-90 camera stations; TEAM Network 2011). Simulations showed that to increase the accuracy it is usually more efficient to increase the number of camera stations than to increase the number of survey days (e.g. Linkie et al. 2007). This can be done by setting camera traps in multiple blocks; for example, TEAM protocol allows for deploying three consecutive blocks of 20-30 cameras, each block operating for at least 30 days (TEAM Network, 2011). With preliminary data on captures, one can use the simulation capabilities of software such as GENPRES (Bailey et al., 2007) to estimate the optimal number of survey days and camera trap stations.

3. Capture-Mark-Recapture (CMR)

For species with individually-distinct fur patterns or artificial marks, data from camera trapping can be analysed with a closed capture-recapture model framework, to estimate abundance and density (Karanth and Nichols, 1998). These models account for the fact that not ne-

cessarily all animals in the study area are observed. CMR approach relies on individual recognition of members of the study population based on coat pattern. However, the method has also been applied to estimating abundance of species that lack natural marker but have phenotypic and/or environment-induced characteristics (Noss et al., 2003; Kelly et al., 2008). This would be acceptable when all individuals within the sample have a unique marker, a scenario that is unlikely when the sample size is sufficiently large for reliable abundance estimation with CMR, as individuals that lack obvious natural markings increases with the sample size. Researchers conducting CMR of species without natural markings should thus clearly indicate how they dealt with ambiguous photographs, stating how many captures are unidentifiable and explain whether or how they included them in the abundance estimate (Foster and Harmsen, 2011).

Camera traps producing high quality photos in terms of clarity, sharpness (moving objects should not be blurred) and resolution are critical even more for species which have not easily distinguishable coat patterns (e.g. rosettes in Eurasian lynx) and for those that lack individually identifiable natural marker. Furthermore high quality pictures are a prerequisite for pattern recognition software (e.g. Bolger et al. 2012; Hiby et al. 2009; <http://www.conservationresearch.co.uk/lynx/lynx.htm> [3 February 2013]), which are progressively more used as camera trap studies extend in sampling effort both temporally and spatially. Thus the ideal camera trap for CMR studies should have a Xenon white flash that has at least two flash distances settings, a short delay between consecutive pictures (currently up to 30 s are necessary for the flash to recharge) and a high trigger speed.

In terms of camera placing, camera traps should be placed at optimal sites in pairs in order to photograph both flanks of the focal species passing by, and maximize the chances of identification. Careful placement of the camera trap is necessary to maximise image quality and preclude the chance of a “skewed” animal image that can reduce similarity coefficients when pattern recognition software are used for individual identification (Kelly, 2001). As the flash of the opposing camera can cause overexposure of the image it is necessary to avoid setting the camera traps exactly facing each other. This problem would be avoided with shutter speed faster than in current models, which would prevent overexposure by the opposing flash. Abundance estimation is still possible with a single device per site, but additional uncertainty associated with individual identification combined with small sample size results in very imprecise estimates (e.g. Negrões et al. 2012). Double camera traps placement enables the user to combine the non-overlapping advantages and disadvantages of different camera trap types. In this regard it would be useful to combine an IR camera trap, which is more sensitive and allow multiple photos per trigger, with a Xenon white flash camera trap. Besides obtaining high quality pictures, this would enable to have an increased detection probability of family groups or individuals following each other very closely.

Study design needs to consider both the spacing of traps relative to individual movement, and the total size and shape of the trap array (Foster and Harmsen, 2011). An important requirement of CMR is that each target species individual must have some probability of being detected (although not all animals may in fact be caught during the survey) and thus there should be at least one sampling site per smallest home range of the target species in the sampled area (Karanth and Nichols, 1998), resulting in an upper limit to possible trap spacing. In addition, if trap spacing is too wide, most animals will only be captured at a single trap, and little or no information on movement will be gained. Further, the overall area sampled by camera traps should be large enough to capture the full extent of individual movements. Another rule of thumb is to set more than one camera trap site per minimum home range of the target species, especially when the species occurs at low density, for example four cameras per home range were set in a study on the Eurasian lynx *Lynx lynx* (Zimmermann et al., 2013).

Given that only a fixed number of camera traps is normally available, researchers face a dilemma with regard to trap spacing: an increased trap density is likely to increase the capture probability of individuals exposed to camera traps, thus increasing capture-recapture rates;

on the other hand, reduced trap density can potentially sample a larger number of individuals. According to White et al. (1982), to get reliable abundance estimates with non-spatial closed population capture-recapture models the overall capture probability should be greater or equal to 0.1, and the overall sample size should be >20 individuals. If there is no data on target species movements in the area, we recommend following the practical recommendation of Karanth et al. (2011), i.e. to potentially expose 10-30 individuals of the target species to camera trapping, ensuring that there are no holes in the sampled area. In the case that more camera traps become available afterwards, trap density can be improved to increase capture rates. Regular arrays of traps which maximize the ratio of sampled area size to its perimeter (= circular shaped sampled areas) are preferable to reduce the edge effect caused by captured individuals moving in and out of the area surveyed over the course of the study (Foster and Harmsen, 2011).

Relevant software for estimating abundance with regular closed CMR models are program CAPTURE (White et al., 1982; Rexstad and Burnham, 1991), as well as the more recent program MARK (White and Burnham 1999; <http://warnercnr.colostate.edu/~gwhite/mark/mark.htm> [3 February 2013]). Recently, a method that uses the location-specific individual capture histories, to construct a spatial capture-recapture (SCR) model was developed by Efford (2004) and Royle et al. (2009a,b). SCR explicitly models individual movement and distribution in space, relative to the trap array, and thus circumvents the problem of estimating the effective area sampled inherent to the regular CMR models, as the trap array is embedded in a large area called the state space. SCR modelling is becoming the method of choice (Nichols et al., 2011) because it considers animal movement explicitly, it allows incorporating site-specific and individual covariates, and it is not biased by an informal estimation of the effective sampling area (Sollmann et al., 2011). In addition, it allows higher flexibility in the sampling design as it performs well across a range of spatial camera trap setups and animal movements, and it is much more robust to changes in trap array size than CMR models (Marques et al., 2011; Sollmann et al., 2011; Zimmermann et al., 2013). Likelihood-based inferences can be obtained with the R package *secr* developed by Efford (2011) and Efford et al. (2009; <http://www.otago.ac.nz/density> [3 February 2013]), and the software SPACECAP has been recently developed to implement flexible Bayesian approaches (Gopalaswamy et al., 2012).

4. Random Encounter Model

This method, proposed by Rowcliffe et al. (2008), aims to estimate density of species that cannot be identified to individual and is based on the likelihood that the camera detection zone (as measured by a cone of known angle and arc) is crossed by passing animals. The method has been developed from tests in semi-captive conditions, and the field trials that have been published are still limited (Rovero and Marshall, 2009; Manzo et al., 2012). Methodological refinements are under development (Rowcliffe et al. 2011; M. Rowcliffe personal communication) and it is likely that it will be increasingly adopted given that this method aims to address a fundamental question in ecology. However, given the method is at an early stage of field testing, our indications should be considered preliminary and subject to validation once wider applications will become available.

Camera traps with fast trigger time and large detection zone will be appropriate, as they will yield a greater number of detections. Also, cameras capable to shoot rapid burst of photos, or to take videos with fast trigger times will allow the measurement of the distance crossed by animals within the camera view in a given time. This information, in turn, can be used to derive the animal's “day range” or “speed of movement” which is an input parameter in the formula that estimates density (see equation 4 in Rowcliffe et al. 2008). No-glow flash and silent camera traps (i.e. not emitting ultrasound) will ideally be needed to cause minimum disturbance and hence not to alter the speed and trajectory of animals passing in front of the camera.

The method needs robust data-set to provide reliable abundance estimates; hence, the number of placements and total number of sightings are the key determinants to its appropriate application. M. Rowcliffe

Table 2 – Summary reference guide of currently available and most used passive infrared sensor (PIR) camera traps for wildlife surveys by cost range. All prices are indicative and subject to change by manufacturers. In the row below each model is the camera trap type (flash technology and trigger speed; IR = infrared).

High end (US \$ 550–1000)	Mid range (US \$ ~450)	Low end (US \$ <250)
Reconyx PC800/850/PC900/950 IR white LED flash, 0.3 s	Reconyx HC500/550, HC600 IR flash, 0.3 s	Bolymedia Scoutguard SG560D white IR flash + Xenon flash, 2 s
Pixcontroller Raptor IR flash, 1 s	Uway UM562 IR flash, 1.7 s	UWAY UV532 IR flash, 1.3 s
Digitrap Xenon white flash, 1 s	Welthar multipir H320 triple PIR sensor, IR flash, 1 s	UWAY UV535 IR no glow flash, 1.3 s
Pixcontroller DigitalEye 12.1 Trail Camera IR and Xenon white flash, trigger speed not available	Spypoint FLA dual Xenon white and IR LEDs flash, 0.45 s	UWAY UM535 IR no glow flash, 1.3 s
Buckeye Cam X7D/X80 IR flash, 2 triggers in 0.1 s		Moultrie M80 or M100 IR flash 1.6 or 1.7 s
Buckeye Cam Orion IR flash, 0.2 s		Cuddeback Attack IR and Xenon flash, 0.25 s
		Cuddeback Ambush IR and Xenon flash, 0.6 s
		Bushnell Trophy Cam HD IR flash, 0.6 s
		DLC Covert Reveal Xenon white flash, 1.2 s

(personal communication) suggests a minimum of around 50 placements, run for long enough to record a minimum of around 50 independent records. As mentioned for occupancy, cameras can be placed sequentially within an acceptable period of time, to reach the required number of placements. Failure to achieve this will decrease the precision of the estimates. In terms of spacing, there are no strict requirements, although obtaining independent records implies that cameras should be spaced enough so to avoid sampling the same individuals repeatedly. It is also critical to place cameras randomly relative to animal movement (or randomly-stratified according to habitats), for the same reasons described for occupancy, i.e. not to bias abundance estimates towards areas of greater abundance than average.

Review of currently available camera trap models and the “ultimate camera trap” for wildlife research

Despite the wealth of camera trap models, there are very limited data available on the strength and weaknesses of models for the purposes of scientific research. An intrinsic limitation is that camera trap models are continuously changing and by the time publications are out the knowledge is dated. In addition, proper assessment of camera traps is potentially expensive and time consuming, requiring laboratory testing and the inclusion of many camera models. Hence, there is a need to develop standard procedures for testing camera traps for scientific research that can be compiled in databases and made widely available through the web.

As notable exceptions, Swann et al. (2004) evaluated 6 models of camera traps to provide guidance on suitability of certain models for specific studies. Field trials of 6 camera trap models have also been carried out more recently (Hughson et al., 2010), and found greater variation between models than reported by Swann et al. (2004). Weingarth et al. (2013) attempted to determine suitable camera traps for estimating Eurasian Lynx abundance and density by CMR, and proposed a process for testing new camera trap models. They tested 6 digital camera models (Bushnell TrailScout 119935, Cuddeback Capture, Cuddeback Capture IR, Cuddeback Expert C3300, Reconyx RC45 and RC60) – under controlled laboratory and uncontrolled field tests – with regards to trigger speed and the image quality necessary for visual identification of lynx moving along trails. Only one camera trap (Cuddeback Capture) proved to be suitable for CMR studies of the Eurasian lynx. Table 2 presents a selection of currently most adopted camera traps for wildlife research.

Through a survey of 154 researchers using camera traps around the world, Meek and Pittet (2012) summarised some of the important fea-

tures of the “ultimate camera trap”, which included: 2 photos taken within 1 s with 0.5 s latency to first trigger, ≥ 5 Mega pixel resolution, 1-100 images per trigger, frame rate interval of 0 to 60 s, time lapse function, aperture controls for close up and distant detection, dual flash systems, flash intensity control, HD video with sound (Tab. 3). They also highlighted some additional requirements such as remote viewers with detection zone water marks, wide PIR detection sensors, battery meters and included a range of suggested housing and locking systems to improve field deployment. Whilst packaging all of the features outlined by these authors into one device would be challenging and prohibitively expensive, all of these suggestions are well founded and desirable. The challenge is in maintaining the cost affordable so that researchers can still purchase the number of units needed for robust scientific research. Many of these requirements will likely become available in future years, and recent models have been manufactured by Reconyx and Scoutguard taking into account the list provided by Meek and Pittet (2012), highlighting the influence users can have in future models.

Conclusions

While camera trap technology has made impressive progress in recent years, there are critical limitations with current technology. These include: (1) detection of camera traps by animals. Our experience indicates that no camera trap remains completely unnoticed by animals, as even professional Reconyx IR models with “no glow” flash are noticed or heard by the animals. Some species can see the IR flash and/or hear ultrasound generated by cameras. (2) In many models, both white and IR LED flashes are not powerful enough to allow a fast shutter speed resulting in blurred photos. (3) There is a need for all digital camera traps (IR, Xenon and LED white flash) to adjust flash intensity automatically to the distance of the subject to avoid overexposed photos. (4) Digital IR camera trap with high quality pictures which allows multiple-photos per trigger should be developed. (5) Passive motion detectors do not have a 100% detection (when two passive camera traps are set at the same site some animals detected by one camera trap will not be detected by the opposite camera). Thus more commercial camera traps with active motion detector should be developed in the future. (6) During day time conditions, images of moving animals taken without flash are often blurred, because of too long shutter speed; this also happens in poor day light conditions, such as at dawn and dusk, when the flash operates but the background is not dark enough; hence, digital camera-traps that automatically adjust shutter speed should be developed in the future.

Despite these limitations, camera trapping remains an exceptional tool for sound scientific inference providing that studies are properly

Table 3 – Some of the camera trap design specifications outlined by 154 researchers (after Meek and Pittet 2012).

Feature	Specification
Trigger speed	Latency to first photo 0.5 s, two photos per s (near-video speed).
Photo speed	At least two frames per s for IR LED flash and one per s with white LED flash.
Image resolution	Programmable resolution 1.3–12 Mp.
Frame-rate intervals	0–60 s between images.
Photos per trigger	Programmable 1–100.
Delay after triggering	At intervals given in seconds or minutes.
Programmable time-lapse trigger	Ability to program in standard or time-lapse mode, which allows the programming of the camera to take a picture at even time-lapse intervals until it picks up a motion, after which it switches to standard mode, recording the events, and back to time lapse at the end of the motion. Capacity to program detection-time periods to just day or just night or between selected hours of the day.
Dual-flash system	White LED – and IR LED – flash system, allows dual-flash capabilities with greater illumination and clarity at night when needed. 990–1000 nm IR LED spectrum.
Video length	HD high definition video in MPEG4 format, duration adjustable between 10 and 60 s or can be programmed to continue until the motion stops.

designed and the adequate camera system is used. While data analysis and management are beyond the scope of this review, the technological advancement in camera trapping is being paralleled by sharp progresses in the development of analytical frameworks (review in Nichols et al. 2011); see also O'Brien et al. (2010); Kinnaird and O'Brien (2012) for species richness and occupancy analysis; Rowcliffe et al. (2011) for REM; Bengsen et al. (2011) for a Generalised Index Approach; Schaub et al. (2004) for multistate CMR models; Gardner et al. (2010) for SCR models for open populations.

Besides applications for wildlife research, a range of other uses have long been made or are recently developing. Indeed camera traps have long been used by hunters in the US and then elsewhere in western countries to keep records of quarry, target species reproduction and to enhance probabilities of hunting success. Today their uses include covert surveillance of people involved in illegal activities such as theft, poaching, arson and trespass. In Australia camera traps are widely used by farmers to detect cattle rustlers and illegal hunters on their property. In the national reserves systems they are used to monitor human activity in sensitive areas as well as early detection of wildfires.

Camera trapping is also emerging as a powerful tool in citizen science, encouraging participation by the community and groups such as schools to contribute to the collation of ecological information on species within their local area. In Saguaro National Park, USA, the national parks service has been running a program called BIOBLITZ where camera traps are used as one of the biodiversity sampling tools (<http://www.nps.gov/sagu/bioblitz-2011.htm> [28 April 2013]) Participants are trained on the use of camera traps and they then deploy them throughout the landscape. In Trento Province, Italy, a network of passionate camera trappers routinely collect data on brown bear and other species around the province, with data being used by the wildlife management authority for monitoring purposes. Similarly, camera-trapping monitoring of lynx is done in Switzerland and it relies to a large part on a network of passionate camera-trappers (game-wardens, hunters, nature lovers). Appropriate training is given to all members of the lynx group.

Camera traps can also play a role in raising environmental awareness of local communities and building conservation management capacity. Images and videos recorded by camera traps are used as an educational tool by many conservation agencies to encourage community participation in species management and forest protection, or simply to enhance communities' environmental awareness by presenting images of animals otherwise unseen by most people. For example Thomas (in review) has been using camera traps in Papua New Guinea to gather image data on two critically endangered tree kangaroos (*Dendrolagus scottae* and *Dendrolagus pulcherrimus*). Local villagers are involved in the programme, and through participation in surveying these rare species have formed cultural ownership and pride for them. Camera traps are now a cultural tool for these villagers to encourage conservation and education of other tribes about the importance of protecting their endemic species.

With the diffusion of camera trapping in a vast range of settings, legal aspects related to protection of citizens' private sphere are becoming

a sensitive issue. Restrictions on the deployment of camera traps have already been introduced in some countries like Austria and Switzerland (Butler and Meek, 2013). There are considerable legal issues related to privacy of people that can impact on camera trapping studies and the implications will vary according to countries' policies. ☹

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Appendix

Annotated list of useful web sites.

<http://www.atrium-biodiversity.org/tools/camerabase> Camera Base, a free software for managing camera trap data.

<http://www.teamnetwork.org/protocols/bio/terrestrial-vertebrate> Terrestrial vertebrate monitoring protocol adopted by TEAM (Tropical Ecology, Assessment and Monitoring Network).

<http://uk.groups.yahoo.com/group/cameratraps> Camera trap email discussion group.

<http://www.trailcampro.com> Detailed reviews, comparisons and technical details on various digital models

<http://www.chasingame.com> Detailed reviews on different camera trap models.