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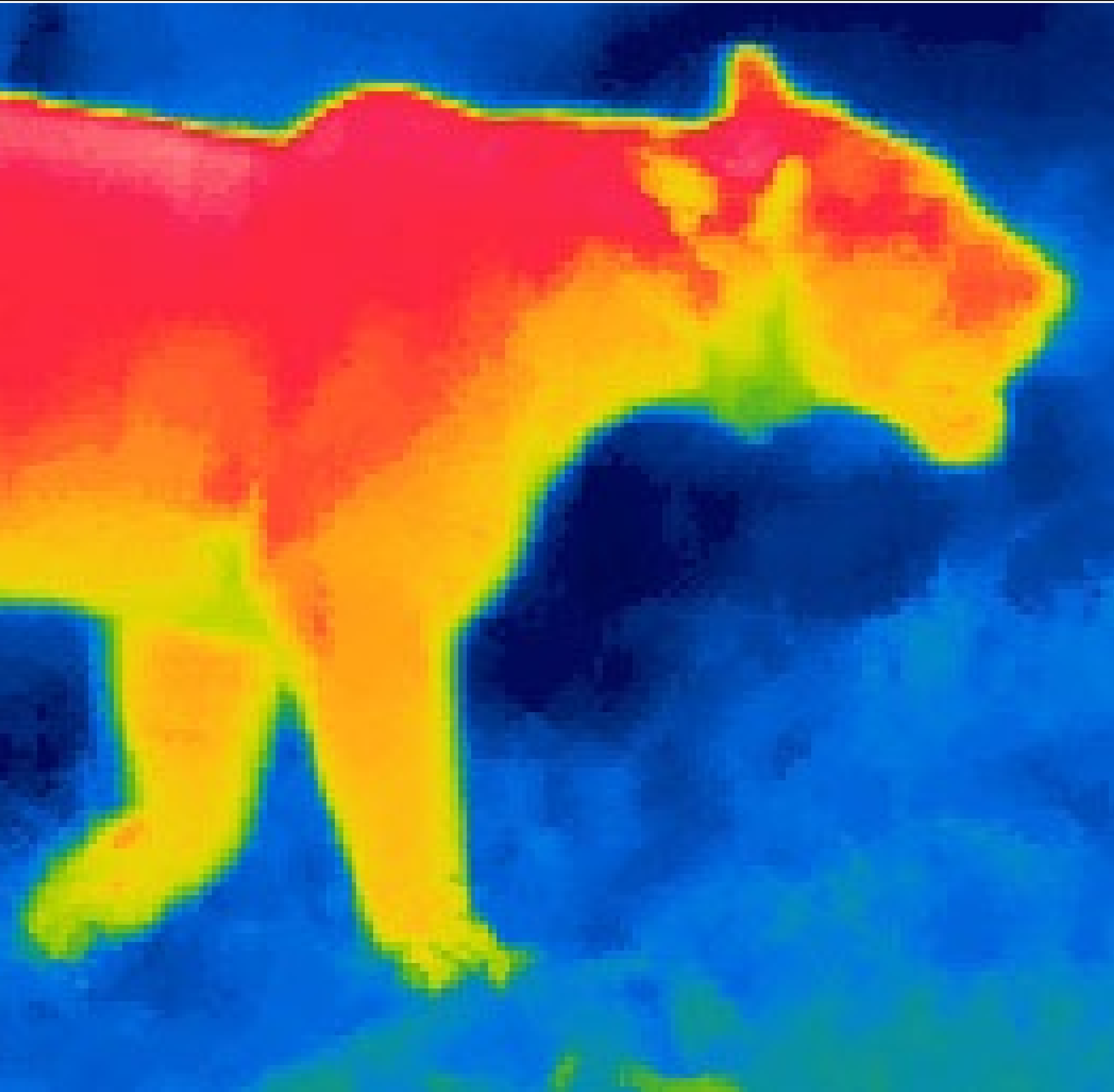
CONSERVATION TECHNOLOGY

CAMERA-TRAPPING



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CONSERVATION TECHNOLOGY

CAMERA-TRAPPING

Camera-trapping for conservation: a guide to best-practices

Oliver R. Wearn & Paul Glover-Kapfer. 2017.
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WWF is one of the world's largest and most experienced independent conservation organizations, with over 5 million supporters and a global network active in more than 100 countries. WWF's mission is to stop the degradation of the planets natural environment and to build a future in which humans live in harmony with nature by conserving the worlds biological diversity, ensuring that the use of renewable natural resources is sustainable, and promoting the reduction of pollution and wasteful consumption.

Cover Image: Thermal image of *Panthera tigris* © Judith Stryker

CAMERA-TRAPPING FAQ

What is a camera trap and how is it different to a time-lapse camera?

The modern digital camera trap is simply a digital compact camera sensor wired up to a passive infrared sensor which is able to "see" the infrared radiation given out by warm-blooded animals. However, any camera which is triggered by an animal to take pictures can be classed as a camera trap. This could include cameras triggered using any of a whole range of different methods, such as trip-wires, pull-wires, pressure plates, lasers or microwave sensors. A camera which is triggered remotely by a human is not a camera trap, and neither technically is a camera which is programmed to take pictures at set intervals, i.e. a time-lapse camera. The term "remote camera" is sometimes used to include this broader class of cameras, which are triggered in the absence of a human operator (but not necessarily by an animal). Other names for camera traps (mostly used in the hunting market) include game cameras, scouting cameras, or trail cameras.

How expensive are camera traps?

Off-the-shelf camera traps range in price from ~$50 to more than $1000 and, as ever in electronics, you get what you pay for. Typical mid-range camera traps suitable for robust scientific monitoring cost $300-500, with more expensive units typically having better detection circuitry, increased reliability, and more customisable settings. High-end camera traps can cost $500-1000, and may have video modes with a fast trigger speed (i.e. a short delay between sensing an animal and starting the recording) or be able to send images over mobile phone or wireless networks. Custom DSLR camera traps, which are necessary to take the highest quality images possible, can easily cost a few thousand dollars if bought new, and are a significant time investment to build and test.

What animal groups can camera traps be used for?

Almost all commercial camera traps sense animals using a passive infrared sensor. This sensor looks for sudden changes in the surface temperature of the environment in front of it, which could indicate the presence of an animal. These camera traps are best suited to anything that has a heat signature (i.e. body size and surface temperature) similar to a deer. This is because technological developments in the commercial camera trap market are still largely driven by the North American hunting market. Luckily, lots of animals have a heat signature sufficiently similar to a deer that the modern camera trap is useful for sampling a wide range of medium- to large-sized mammals and birds. The lower body size limit for camera traps used to be around 1 kg, but most mid- and high-end passive infrared sensors can now detect animals as small as 100 g, provided they are within 2 m. Beyond mammals and birds, passive infrared sensors have also been used to successfully detect reptiles (including small skinks, snakes, varanid lizards, and crocodiles). However, special approaches will usually be necessary in this case, and detections are unlikely to be as reliable as for mammals and birds. Other sensor types, such as active infrared sensors and pressure plates are alternative options when passive infrared sensors fail, albeit at greater cost. In addition, new software-based methods, such as pixel change detection, could expand camera-trapping into the aquatic realm in the near future, to monitor fish and marine mammals.

Can camera traps be used for monitoring animal abundance – will I be able to tell individual animals apart?

Camera traps can be used to monitor a host of different ecosystem variables, such as the abundance, diversity and distribution of animals. Abundance monitoring is particularly effective with camera traps and has also been shown to be cost-efficient relative to rival methods (such as line-transects or live-trapping) for longer-term projects. It is often now the top choice of wildlife biologists, even for monitoring the rarest mammal and bird species in a community. A number of approaches can be used to monitor abundance. Most simply, the trapping rate (number of photos per unit of sampling effort) can be used an index of relative abundance, to compare trends across space or time, albeit with some important caveats. More robust methods include mark-recapture modelling (for species which can be individually-identified in images), and random encounter modelling (for species which cannot be individually-identified). In order to be able to indentify individual animals in images, they need to have unique markings, such as the stripes of a tiger or a zebra. You also need to use a camera trap which can take clear photos of the animal markings (in most cases, you will need a camera trap with a white flash, not an infrared flash). The random encounter model was originally formulated specifically with camera-trapping in mind, and requires some additional knowledge of the system, including the movement speed of the focal species and the detection zone characteristics of the camera. This requires additional fieldwork to make these measurements in the field. However, new methods are currently being trialled in order to be able to extract these from the camera trap images themselves.

How many camera traps should I buy?

Most often, the answer will be “as many as you can possibly get your hands on!”. The number of camera traps you have will determine the amount of data you can collect, and therefore which statistical methods it will be possible to apply. In practice, a better question to ask is “what is the minimum number of camera traps I need to achieve my objects?” This can be estimated approximately using information on your ideal survey design, how long it will take to set up camera traps (which will depend on how accessible your study sites are), and how quickly you need to complete the survey (e.g. to meet certain model assumptions, or due to the availability of resources). If you can afford (or can borrow) your estimated minimum number of camera traps, then your study is more likely to be a wise investment of scarce conservation resources. If you cannot meet the minimum required number of camera traps, then you should stop and seriously consider if you need to re-evaluate your study’s objectives. Even though there may be momentum building in your project, you should strongly avoid the temptation to just proceed regardless.

What camera trap model should I buy?

Commercial camera traps are all broadly similar in basic form – being a compact digital camera, triggered by a passive infrared sensor – but they do nonetheless vary in a large number of important ways. Principle among these, are the characteristics of the detection circuitry (how sensitive the passive infrared sensor is, and how quickly the camera can take a picture after sensing an animal), whether they have an infrared or white flash, and whether they are able to send data remotely or not. The camera trap model most suitable for you will depend on what you intend to use it for. For example, if you intend to do random encounter modelling, you will need a camera with a fast trigger speed and, ideally, an infrared flash. If you intend to carry out a mark-recapture survey you will instead most likely need a camera with a Xenon white flash. Ultimately, given the vast number of models on the market today, and the rapid pace at which they are updated by manufacturers, it is difficult to make a single recommendation for which camera trap model to buy. A sound knowledge of how camera traps work, and the key ways in which camera traps differ, will guide your purchasing decisions.

Can camera traps record video?

Not all commercial camera traps can record video, but an increasingly large number do. In most of the camera traps that record video, you simply choose which mode you want to use. Some models also offer a hybrid mode, which takes a single picture and then starts a video straight after. Note that video modes are slower than image modes, and you may therefore miss some animal detections altogether. They should therefore be used with caution in robust scientific monitoring. Video files also take up much more hard disk space than images, and are more difficult and laborious to process. Most camera trap software programs do not currently support video. A compromise between image and video is to use a camera trap capable of shooting in a "near-video" mode, in which rapid sequences of images (< 1 second apart) are taken.

Can I buy a camera trap which sends me the data remotely, so that I don't have to physically go and get the data?

Most camera traps available on the market today are autonomous, in that they work offline and on their own, according to the settings you have applied during setup. However, an increasing number of "networked" cameras are becoming available, which can send data over mobile phone or wireless networks. Camera traps on mobile phone networks typically send images to a mobile phone number or e-mail address, whilst wireless camera traps send images to a central base-station (which, in some systems, is itself networked). Some manufacturers are also experimenting with systems in which each camera trap can pass images along the network in a "daisy-chain", meaning that only one camera needs to be checked to retrieve all the data. Networked cameras can also typically be contacted mid-deployment, to check on their battery and memory status, and change some of the key settings. Networked cameras have the potential to vastly increase the efficiency of camera-trapping (in particular, because cameras are only serviced when required), and increases the usefulness of camera traps for certain uses (such as anti-poaching). However, you should be aware that networked cameras are still very much in development. They are expensive and usually do not send all of their data remotely (typically only low-resolution images, and no videos). Camera traps which use mobile phone networks incur costs for sending data, and may not work on networks outside the US and Canada, or in areas with poor signal strength.

What settings can I adjust on a camera trap?

Most camera traps offer the same basic settings that a user can adjust. These include: the sensitivity of the passive infrared sensor (usually offering high, medium and low settings); the sleep time between successive triggers (which can be useful in some instance to avoid having the memory fill up too quickly with repeated images of the same animal), whether images or video should be taken; the number of images (and time interval between them) or length of video to take for each trigger event; the image size or video quality, and whether the camera trap should only sample during the day/night or 24 hours. Mid- and high-end cameras will give the user access to more customisation, such as: setting the device to operate only at certain times or on certain days; entering an anti-theft passcode; stamping images with a custom label (such as the camera name or location), and finer control of exposure, ISO and shutter speed.

How should I set out my camera traps?

How you should set out your cameras depends very much on exactly what it is you want to achieve. For informal inventory work, i.e. just building up a species checklist of an area, you are more-or-less free to place cameras as you see fit. However, for more robust scientific monitoring (for example of species diversity, abundance or distribution), then clear best-practice guidelines exist. In general, standard principles of sampling theory should be adhered to as much as possible, including randomisation of sampling locations and division of your study sites into sampling strata.

How long should I leave my cameras out for before checking or moving them?

The simplest answer to this question is that you should check a camera trap just as the battery dies or the memory card fills up. This maximises the amount of data it collects. How long a camera trap lasts depends on its resting and peak power consumption (mid- to high-end cameras are very efficient devices), what kind of batteries you put in it, how many batteries you put in it, the ambient temperature of the environment, how large the memory card is, and lastly how much animal activity there is in front of the camera. Some camera trap manufacturers give estimates of the typical number of images their cameras can record on a single set of batteries (e.g. 20,000-50,000 images for Reconyx Hyperfire camera traps). In practice, camera traps tend to last anywhere between 3 weeks and 6 months, depending on all the factors outlined. However, when doing robust scientific monitoring, it is not always possible to leave a camera out until its batteries or memory are exhausted. This is because only a limited number of camera traps are usually available for a study, and they have to be moved relatively frequently in order to cover a sufficient number of sampling points. In this case, how long you should leave a given camera trap in place depends very much on your objectives, as well as the characteristics of your study species (how common it is, and how detectable it is if present).

How can I manage and analyse the data – are there software packages available?

Good systems for managing and analysing camera trap data have traditionally been sorely lacking, which has meant that far too much hard-won data has remained untouched on hard-drives. Happily, there has recently been frantic development in this area, and various dedicated software packages for camera trap data have been released. Variously, these packages help with processing image or video data, creating a relational database to hold all the data (including data on sampling effort and any covariate data, such as GPS coordinates and environmental data), and conducting analyses. However, each of the available packages has strengths and weaknesses, and no single package has yet received substantial “buy in” from the camera-trapping community. For small-scale or short-term surveys, it might not always be worth the set up costs of using dedicated camera trap software. It might be more efficient to just tag images with information (such as species identifications) using image-editing software (e.g. Adobe Lightroom), maintain a few spreadsheets of data, and conduct analyses using Microsoft Excel in combination with the required stand-alone programs (such as PRESENCE for occupancy, or MARK for mark-recapture).

Do I have to go through all my images manually, or can I get a computer to do it?

Great question! For the moment, the answer is that human eyes will indeed have to manually look through all your images. This can be a very laborious process, taking weeks or even months. The good news is that various recent projects have demonstrated that there exists a highly motivated global army of citizen scientists willing to look at your data (e.g. on the Zooniverse platform, which allows any camera-trapper to start a new project). This is not without substantial set up and maintenance costs (for example, to recruit volunteers and then keep them engaged, and to validate their identifications), but may save considerable time for large camera trap projects. Computers are still nowhere near as good as humans at identifying species in camera trap images, but various research groups are actively working on this problem. The future of camera-trapping will undoubtedly involve a major role for open-source machine-learning algorithms in the processing of data.

Camera traps can be left in the field to continuously watch an area of habitat for weeks or even months, recording the rarest events which occur in nature. This can include everything from the raiding of a bird´s nest by a predator, to a big cat patrolling its territory.

Image of a leopard, *Panthera pardus*: © Will Burrard-Lucas

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PREFACE

1-1 Why is this guide needed?

Camera traps have emerged as a powerful tool for a range of purposes, and are now ubiquitous in scientific research and applied conservation across the planet. This growth in camera trap use has been accompanied by a significant amount of methodological research, aiming to increase the efficiency of camera-trapping and the quality of data that is produced. Unfortunately, not all of this research is presented in an accessible form (for example, it might be buried in a report or journal article concerned with another topic), and much of it is hidden behind paywalls. In addition, a wealth of anecdotal information on best-practices has also accumulated (for example in e-mails, forums or in grey literature), but this is poorly organised and difficult to find. As a result, many camera-trappers, and especially those new to the technology, are learning through an inefficient and frustrating process of trial-and-error, rather than building on the knowledge that already exists in the camera-trapping community.

There have been a number of recent attempts to synthesise knowledge of camera-trapping best practices, for example in books (O'Connell *et al.* 2011; Ancrenaz *et al.* 2012; Meek *et al.* 2012, 2014a; van Berkel 2014) and scientific papers (Rovero *et al.* 2013; Surnato *et al.* 2013; Burton *et al.* 2015), but many of these have a narrow geographical or subject area focus, are highly technical, or are difficult to access. WWF-UK identified a need to produce freely-available and impartial guidelines for camera-trapping best practices, based on the latest research, and with a global focus. These guidelines should be useful to any researcher or conservation practitioner in the field, giving them all the information they need to quickly deploy camera trap technology in an effective way. The guidelines allow for a broad range of study types (from species monitoring to anti-poaching) and contexts (from rainforest to desert) that camera-trapping could be used in. No prior knowledge of camera-trapping is assumed, although we anticipate that novice and seasoned camera-trappers alike should find the guidelines useful.

The advice and recommendations in this guide are a consensus of best-practice, as taken from the collective literature (published and unpublished) of thousands of camera-trappers. The emphasis in these guidelines is on pragmatic and flexible guidelines which can be applied to most situations, with a necessary trade-off in terms of specificity for any given study. Readers should therefore be aware of the need to critically evaluate the guidelines, and adapt them to their local context as they see fit. In addition, methodological studies of camera-trapping are still in their infancy, meaning that aspects of the guidelines remain a "best guess" based on the evidence to hand. Where conflicting evidence currently exists, we have made this clear and presented the evidence on all sides.

1-2 The structure of this guide and how to read it

Depending on your prior experience with camera-trapping, and what you are hoping to take away from the guidelines, we encourage you to only read the sections of this guide that are most relevant to you (**see Table 1-1**).

After setting the scene with the history of camera-trapping (**Chapter 2**) and a warning about their drawbacks (**Chapter 3**), the guide provides essential information on how a camera trap actually works (**Chapter 4**) and what they can be used for **(Chapters 5 and 6**). These Chapters should also be useful to anyone deciding if camera traps are a useful technology for their requirements.

The next two Chapters are designed to help with planning a camera trap study. Specifically, we discuss recommended survey designs, depending on the aims of the study (**Chapter 7**), and provide advice on what kind of camera trap to buy, as well as how many (**Chapter 8**).

We then provide a 10-step guide to executing a camera trap study from start to finish (**Chapter 9**) and discuss the practical realities of camera trap work in the field (**Chapter 10**). These Chapters will be essential reading for anyone running a camera trap study in the field.

Finally, we provide recommendations on how to manage (**Chapter 11**) and analyse (**Chapter 12**) camera trap data. These Chapters will be especially useful reading for anyone tasked with analysing camera trap data. If the analyst is well-versed in sampling theory and the statistical models they will be using, they can probably skip the specifics of how these models relate to camera-trapping (C**hapter 7**).

1. What do you want to do?	2. Chapters you should read				
	Introductory Material (2-4)	What are camera traps good for? (5-6)	Planning a camera trap study (7-8)	Executing a camera trap study (9-10)	Dealing with camera trap data (11-12)
Determine if camera-trapping might be useful in my work	✓	✓			
Understand enough about camera-trapping to review papers and collaborate		✓			✓
Oversee a camera trap study (e.g. as a manager)	✓	✓	✓		✓
Run a camera trap study in the field (e.g. as a field technician)	✓		✓	✓	✓
Analyse camera trap data			✓		✓

Table 1-1. Which Chapters of the guide should I read? After identifying what it is you hope to achieve with this guide (1), read along to find out which Chapters will be most relevant to you (2).

1-3 What this guide is not about

The guidelines provided here primarily cover the planning and execution stages of a typical camera-trapping study (**Fig. 1-1**). This includes planning the sampling design, choosing the equipment, carrying out the field work and managing the incoming data. We only lightly touch on the formulation of a study's aims and objectives (**Chapter 7-1**), as well as the analysis of camera trap data and making inferences (**Chapters 7 and 12**). We do not provide details on the statistical machinery behind the various models discussed, nor do we provide walk-throughs of how to analyse data. Instead, we refer the reader to primary sources for this information (see the citations and recommendations for further reading in the relevant Chapters), as well as options for getting help (such as help forums and e-mail lists).

We have also deliberately avoided recommending specific camera trap models in this guide. This is because the market changes so rapidly each year as manufacturers advance the technology and release new models. Instead, we provide all the information required to understand the differences between camera trap models, and the features required for a given type of study.

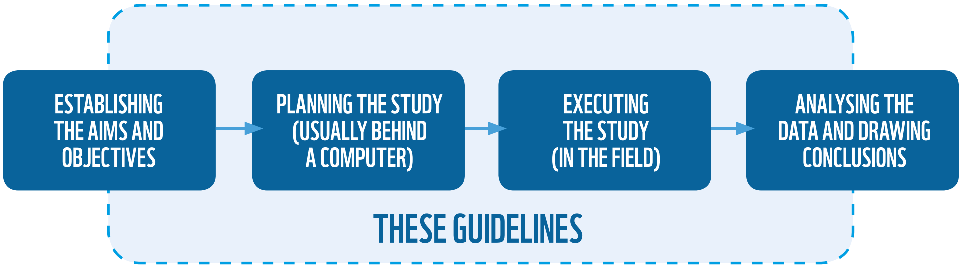


Figure 1-1. The best-practice guidelines provided here primarily cover the planning and execution of a camera trap study. Other sources of information should be consulted for establishing the aims and objectives of your study and analysing the data.

Over the last decade, millions of people around the world have become aware of the camera trap. The candid images and videos that camera traps produce have been featured in countless documentaries, are widely shared on social media, and have been the focus of hugely popular citizen science projects. Less well known is the fact that the camera trap has a long history that extends back more than 100 years.

Image of a Bornean orangutan, *Pongo pygmaeus*: © Oliver Wearn

2

THE EVOLUTION OF THE CAMERA TRAP

HIGHLIGHTS

- Camera traps have been in use for over a century and were present at the very beginnings of wildlife photography
- Most early camera traps were large and cumbersome, had mechanical triggering systems, and could only record a few dozen images
- As a wildlife research tool, the camera trap remained the preserve of a select few until the 1990s, when the first commercial units began to be widely used
- The modern digital camera trap came to prominence from the mid-2000s, and is now a standard tool at the disposal of researchers, land managers and conservation practitioners

Camera traps are not a new technology. Cameras that are triggered by wild animals have been in use for **more than 100 years,** pioneered by one of the fathers of wildlife photography, George Shiras. Shiras used wires which, when disturbed by an animal, triggered a camera and a highly explosive magnesium flash. Using these methods, he obtained some of the first images of nocturnal wildlife in the US and Canada. Pioneering the use of both remote triggering and nocturnal photography, he laid the foundations for the modern camera trap.

In the 1920s, these methods were subsequently adapted by two men working on opposite sides of the world. Frederick Walter Champion, a forester in the British Imperial Forest Service in India, used trip-wires and pressure plates to camera-trap the wildlife of the Himalayan foothills. Champion captured the first high quality photos of wild tigers, leopards, sloth bears and other species, and was the first to demonstrate that **individual tigers could be identified** in camera trap images from their stripes (Athreya *et al.* 2014). Meanwhile, Frank Chapman, the first bird curator of New York's American Museum of Natural History, was in Panama carrying out the **first ever species inventory** (as we would recognise it today) with camera traps. Over a period of years, he documented the mammal community of Barro Colorado Island, and produced among the first ever images of wild tapirs, coatimundis, ocelots and pumas. His photos of white-lipped peccary, a species now extinct on the island, demonstrate the value of camera trap images as permanent and verifiable records, much like museum specimens. Inventories at that time were traditionally done using guns and lethal traps, and Chapman remarked that his new camera trap survey method was "a census of the living, not a record of the dead" (Raby 2015), a key benefit of camera traps which is still true today.

It wasn't until the 1950s, however, that camera traps really **began to be explored as scientific** tools for collecting systematic, quantitative data. Gysel & Davis (1956) described perhaps the first instance of this, using a home-made "automatic photographic unit" in a study of seed predation. Seeds were attached to the camera setup with a thread, and when an animal disturbed the seed, the camera shutter and flash were activated. Although this camera had to be manually reset for each exposure, it marked the beginning of a period of rapid development in camera trap technology. From the 1950s until the 1990s, a wide variety of home-made camera setups – including time-lapse cameras, video cameras and true camera traps – were described, in most cases requiring specialist engineering or electronics skills to put together (e.g. Pearson 1959; Dodge & Snyder 1960; Winkler & Adams 1968; Temple 1972; Goetz 1981; Danielson *et al.* 1996). Camera traps during this time were triggered mechanically (using treadles, pull-wires or trip-wires) or with light beams, and typically needed large, heavy batteries to power the flash and any electronics. As a result, most of the camera setups during this time were **time-consuming to setup, and cumbersome to transport.** Abbott & Coombs (1964) noted triumphantly that their camera setup weighed “only 47 pounds” (21 kg), an order of magnitude heavier than the camera traps of today.

Developments in camera trap technology during this period were spurred on by two desires: 1) to observe animal behaviours, such as food provisioning of nestlings by adult birds, **without causing disturbance,** and 2) **to record “hyper-rare” events** such as nest predation, which would otherwise require many thousands of hours in the field to observe with any great frequency, if at all.

Relatively few researchers at this time were using camera traps to study the distribution and abundance of wildlife, the most common use of camera traps today. The exception to this was a study by Seydack (1984), in many ways **the forbearer of the modern camera trap survey,** of mammals in a South African rainforest. Seydack deployed camera traps, which were triggered using a pressure plate, in a systematic sampling grid. Unusually for the time, he also did not use any bait to attract animals. He recorded nearly 600 animal detections of 14 different species during the 3 years of the study, and noted that he could identify individual bushbuck, leopards and honey badgers in the photos based on their characteristics. Griffiths & van Schaik (1993a) advocated similar methods almost 10 years later, **coining the term “camera-trapping”** in the process. In a 3 year study in the rainforests of Sumatra, Indonesia, they turned camera traps onto the problem of assessing human impacts on wildlife for the first time, documenting differences in relative abundance and activity patterns across forest sites with and without human traffic (Griffiths & van Schaik 1993b). Around the same time, the US Forest Service began experimenting with camera traps (in this case triggered using baited pull-wires) for large-scale monitoring of carnivores, such as marten and fishers, in the western US (Zielinski & Kucera 1995).

The biggest innovation during this period of fervent experimentation with camera traps, which remains a key component of the modern camera trap, was the adoption of **infrared triggering devices.** Carthew & Slater (1991) described an infrared trigger consisting of a rapidly pulsing beam of infrared light which, when broken by an animal, immediately triggered the camera. This brought clear advantages over the mechanical triggers which were then common, in terms of both the reliability and precision of triggering. At the same time, developments in rechargeable battery technology were gradually increasing the portability of camera setups, and began to allow for repeated deployments of cameras over longer time periods than just a few days.

Capitalising off the development of cheap, 35 mm film compact cameras, the **commercialisation of camera trap development** began in the late 1980s and led to much more widespread use of the technology. This began with the Trailmaster TM1500 (and later TM1550) systems, which combined an active infrared trigger, similar to the home-made setup of Carthew & Slater (1991), with a compact camera. Although this commercialisation was brought about largely by **demand from the hunting market,** Kucera & Barrett (1992) recognised early on the huge potential of this system for wildlife studies. Indeed, Trailmaster units were subsequently used in two hugely influential papers (topping the list of the most-cited camera-trapping studies ever) which demonstrated that **tiger population density** could be estimated using camera traps and capture-recapture analysis (Karanth 1995; Karanth & Nichols 1998). This work, in combination with the release of cameras that came integrated with **easy-to-use passive infrared triggers,** such as the Camtrakker and DeerCam (later becoming Cuddeback), greatly facilitated the uptake of camera traps by wildlife biologists. There was a flurry of papers at this time estimating the density of different cat species (O’Brien *et al.* 2003; Trolle & Kéry 2003; Kawanishi & Sunquist 2004; Maffei *et al.* 2004; Silver *et al.* 2004), and a number of conservation NGOs quickly adopted Karanth & Nichols’s methods (e.g. Henschel & Ray 2003; Lynam 2003; Jackson *et al.* 2005).

Digital camera traps began to compete seriously with film camera traps from the mid-2000s, having long been limited by poor resolution and slow trigger times. Since then, digital camera technology has consistently improved each year, greatly increasing the quantity of data that can be collected for a given effort in the field. From the 36-exposures possible on the original film cameras, most cameras available today are able to collect **tens of thousands of images on a single set of batteries.** Camera traps became highly-effective data-collecting devices and this allowed researchers to collect usable data on the distribution and abundance of a much wider range of species, including the hyper-rare species. In addition, it provided researchers with much greater flexibility in how they deployed their camera traps in such studies, for example by deploying them with the intention of capturing as many species as possible (without using bait, and possibly off-trail), instead of just a single cat species.

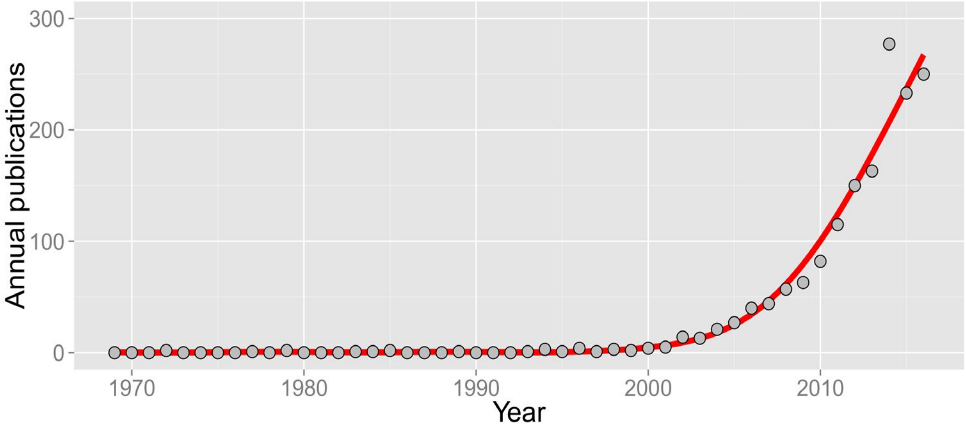


Figure 2-1. Annual number of articles listed in the Web of Science mentioning camera traps (or various other synonyms, such as automatic camera, game camera, or remote camera) between 1969 (the first year of reliable records) and 2016. For the period before 2000, a total of just 25 articles were listed, which is fewer than the annual number of publications from 2005 onwards. The figure for 2016 was extrapolated based on the results up to June of that year.

As digital camera traps were taking over from film cameras, two further developments assured the camera trap's continued rise within wildlife ecology and conservation. Firstly, new methods were being developed which allowed inferences to be made about **species occupancy,** whilst accounting for the fact that a species would sometimes be overlooked (MacKenzie *et al.* 2002; Tyre *et al.* 2003). This opened up the possibility of carrying out robust monitoring of a much wider range of species than was possible using the capture-recapture methods of old. The second development was a shift towards **infrared flash instead of white flash.** Infrared flash reduces the chances of disturbing species and altering their behaviour or movements, and is much more useful for broad-spectrum sampling of wildlife. Although white flash is still popular for capture-recapture studies, because of the clearer pictures it produces for the purposes of identifying individuals, most cameras on the market today have infrared flashes.

Further reading: Kucera & Barrett (2011) give a thorough history of the development of the camera trap from the 19th Century onwards, whilst Cutler & Swann (1999) summarise the rapid period of camera trap development particularly between 1950 and 1990.

Over the course of more than 100 years, the camera trap has gone from a hobbyist obsession for a select few photographers and biologists, to today being a highly effective tool at the disposal of any researcher, land manager or conservation practitioner interested in covert monitoring of wildlife, or even people. Camera traps have been involved in **more than 1,400 publications to date,** and they have been adopted by global biodiversity monitoring initiatives (e.g. Beaudrot *et al.* 2016). The camera trap has now become a firmly entrenched part of modern wildlife ecology and conservation.

Camera traps are highly effective tools for wildlife biologists, especially for monitoring medium- and large-sized mammals and birds. They also produce highly engaging content for outreach and educational purposes. However, they are not a panacea. In these guidelines, we provide the information you need to decide if camera traps are right for your objectives.

Image of a Baird's tapir, *Tapirus bairdii*: © Esteban-Brenes Mora / Nai Conservation

3 THE CAMERA TRAP IS NO PANACEA

HIGHLIGHTS

- Don't start with the premise that the camera trap is the solution, and then look for a problem to solve; instead start by identifying what the problem is you're trying to solve!
- Sometimes, camera traps are not the best option, and other sampling methods may provide similar information more quickly or at lower cost
- If you decide to use camera traps, do not underestimate the significant practical challenges that come with their use, such as dealing with theft and processing large amounts of raw image or video data

Despite this being a guide to camera-trapping, the intention is not to persuade you that camera traps are limitless in their uses and potential. Although it is easy to evangelise about the many benefits that camera traps can bring, they **may not always be the most effective and cost-efficient** tool at your disposal. A common temptation when encountering any new tool is to see everything as a potential problem that it can solve. This kind of inverse reasoning – expressed in the familiar adage "if all you have is a hammer, everything looks like a nail" – is especially attractive with camera traps and the flashy data that they produce. Of course, the best place to start is with **clear and explicit** aims (**Chapter 7-1**), and only then should you identify the best tools to achieve those aims.

Camera traps have certainly been shown to be effective in many situations (see **Chapter 5**, **Table 5-3**), and may indeed be the only practical option for certain tasks, such as recording very rare behaviours. However, examples in the literature show that, **sometimes, money is probably better spent elsewhere** (see **Table 5-3** for examples, such as DNA sequencing of scats and using detector dogs). Where camera traps have failed, this can be an opportunity to critically evaluate the best way to approach a problem, and can also be instructive about major limitations of current iterations of the technology.

There is also a glaringly obvious, though sometimes overlooked, limitation of most camera traps: they are most useful for l**arge, warm-blooded, active and terrestrial animals,** with somewhat limited usefulness for other taxa. Although new developments in camera trap technology, and new ideas for deploying the technology (some of which are featured in this guide), are slowly increasing the range of taxonomic groups for which camera traps are suited, clearly the vast majority of animal diversity is effectively "dark diversity" to camera traps. The fact remains that camera traps serve as a window onto a relatively limited set of species.

Finally, the **practical hurdles** that come with using camera traps (see **Chapter 10**) should not be under-estimated, and can often take new users of the technology by surprise. The **unreliability** of some camera models (especially in harsh environmental conditions) can be frustrating, and it can prove **time-consuming and technically challenging** to extract meaning from a large, and sometimes overwhelming, stream of image or video data collecting on memory cards. In areas populated by humans, the struggle against **theft and interference** can quickly become the deciding factor on whether your study is a success or failure. Throughout this guide, we offer ways of mitigating these problems, but there are obviously substantial opportunities for camera trap technology to improve in future.

Over the last century, camera traps have gone from being an experimental technology used by just a handful of pioneering photographers, to a commercialised technology being used by many thousands of hobbyists, hunters, researchers and conservationists. The modern camera trap – which can be bought off-the-shelf for a few hundred dollars – is a digital camera connected to an infrared sensor which can automatically detect animals.

Image: © Nick Hawkins / Nai Conservation

4 UNPACKING THE CAMERA TRAP

HIGHLIGHTS

- A camera trap is simply a camera which is triggered by the presence of an animal
- Triggers can be directly acted upon by an animal, as in the case of a mechanical treadle, but are mostly now designed to indirectly sense an animal
- Almost all modern camera traps are equipped with a passive infrared sensor, which detects moving objects that differ in their surface temperature to the background scene
- Most camera traps automatically adjust their settings to return a well-exposed and clear image of an animal irrespective of the conditions, and this can have varying results
- The detection zone is the notional area in front of a camera in which it will be able to detect animals, and this zone will vary will depending on the camera, the environmental conditions and the species
- Cameras differ along a large number of dimensions, but the main distinctions are:
  - Compact versus full-frame image sensor
  - White versus infrared flash
  - Networked versus autonomous operation
- Camera traps can be clustered into four broad types – Custom, Budget, Mid- to High-end, and Experimental – and most research is done with Mid- to High-end camera traps, which have an infrared flash and reliable detection circuitry

In this Chapter, we explain how camera traps actually work, which is essential for understanding their strengths and weaknesses (**Chapter 5**), and ultimately for interpreting the data they produce (**Chapter 12**). We also explore the different ways in which camera traps models differ, for example in terms of their functions, size, cost and quality. At the end of this, we identify four broad types of camera trap. An understanding of the broad types of camera trap, as well as the specific feature options available, is the first step towards deciding what camera trap to buy (or borrow) for a given study (**Chapter 8**).

4-1 How do camera traps work?

4-1-1 How are camera traps triggered?

Camera traps come in many guises, and go by many names, including "remote camera", "game camera", and "trail camera". However, all camera traps have in common the property of being **triggered automatically by the presence of an animal.** To achieve this, a number of different types of trigger can be used, broadly separating into those which are **directly acted upon** by an animal, and those which **indirectly sense** the presence of an animal.

Mechanical triggers are the simplest form of a direct trigger, and are physically pushed or pulled by an animal. Many of the earliest camera traps used such triggers, employing trip-wires, pull-wires, treadles or pressure plates. The modern, electronic equivalents of these direct triggers include wireless **pressure pads** (e.g. the PixController Pressure Mat Sensor) and **active infrared (AIR)** sensors, i.e. "break-beam" triggers. Although direct triggers have fallen out of favour for most applications, they remain useful in some special cases. For example, home-made pressure sensors have been used to capture images of otters emerging from cold rivers (Lerone *et al.* 2015) and gopher tortoise (*Gopherus polyphemus*) mating behaviours (Guyer *et al.* 2012), and AIR sensors have been used to capture images of fire salamanders (*Salamandra salamandra*) emerging from their burrows (Leeb *et al.* 2013).

AIR sensors are composed of two parts: an **emitter** which produces pulses of infrared in a narrow beam, and a **detector** (typically placed on the opposite of a trail to the emitter) which records the pulses. When the pulses are interrupted by a passing animal, the detector signals this to the camera and an image is taken. This setup means the location of an animal on triggering can be predicted in advance, and the flash and camera setup can therefore be finely adjusted for artistic effect. This is why AIR sensors, such as the TrailMaster units, remain popular amongst **wildlife photographers** using DSLR camera traps. AIR sensors can also be effective for research purposes where the path used by the target species is **highly predictable** (e.g. snow leopards, *Panthera uncia*: Jackson *et al.* 2005), or where indirect sensors struggle (e.g. ectothermic species, such as the gopher tortoise: Alexy *et al.* 2003). They can also be used to photograph **high-speed events,** such as a bird or bat in flight (Rydell & Russo 2014).

Indirect triggers can detect when an animal is in the vicinity of a camera trap, even if it is at a distance from the device, by sensing various forms of energy which animals emit. Indirect triggers are typically **smalle**r, more **concealable** and **less invasive** than direct triggers. The downside of using them is that the location of the detected animal is less precisely known than with direct triggers.

Almost all modern commercial camera traps (**Fig. 4-1**) are equipped with a specific type of indirect trigger – the **passive infrared (PIR) sensor.** PIR sensors are triggered by moving objects which are a different surface temperature to the background environment. This is often summed up in the phrase “heat in motion”, although objects which are colder than the background are also detected (see **Box 4-1** for technical details on how PIR sensors work). This method of detecting animals makes them very effective for detecting a whole range of **vertebrate species which generate their own body heat,** including birds and mammals, as well as somewhat effective for species which may be periodically hotter or colder than the background environment, such as reptiles. Some PIR sensors can also be triggered by animals as far away as 30 m, and at an angle from the camera up to 35°. However, the detection method of PIR sensors is relatively specific and will miss many species which produce either a weak signal, such as small mammals and birds (but see De Bondi *et al.* 2010), or no signal at all, including most reptiles, amphibians and invertebrates (but see Welbourne 2013). They are also **easily fooled by inanimate objects,** such as the sun, dappled shade (which is moving), or vegetation that has been warmed in the sun and then blown by the wind.

Despite the limitations of PIR sensors, they remain very popular and have almost completely supplanted any other type of indirect trigger. They substantially outperform microwave sensors, which apparently suffer from a lack of directionality (sometimes triggering for animals outside the field of view) and poor sensitivity (Glen *et al.* 2013; Nazir *et al.* 2017). Other potential types of indirect trigger include **acoustic, seismic and magnetic sensors,** as being trialled with the Zoological Society of London’s “InstantDetect” camera trap. These are likely only suitable in specific cases (the InstantDetect camera is primarily for detecting poachers), and the sensors would have to be tuned to the specific cues of focal species to avoid lots of false triggers (e.g. sounds or vibrations in a specific frequency range).

“ZSL InstantDetect” camera trap: www.zsl.org/conservation-initiatives/conservation-technology/instant-detect

Another option for indirect triggering might be to use automatic motion detection in continuous video streams, which would rely on **software algorithms** to “see” when an animal appears (e.g. using pixel change detection) and trigger recording. High-frequency time-lapse imagery could also be used as an alternative to continuous video (Nazir *et al.* 2017), which would reduce the power consumption of cameras, albeit at the cost of increasing the risk of missed detections. This software-based method would be particularly useful in an underwater environment, in which infrared sensors do not function.

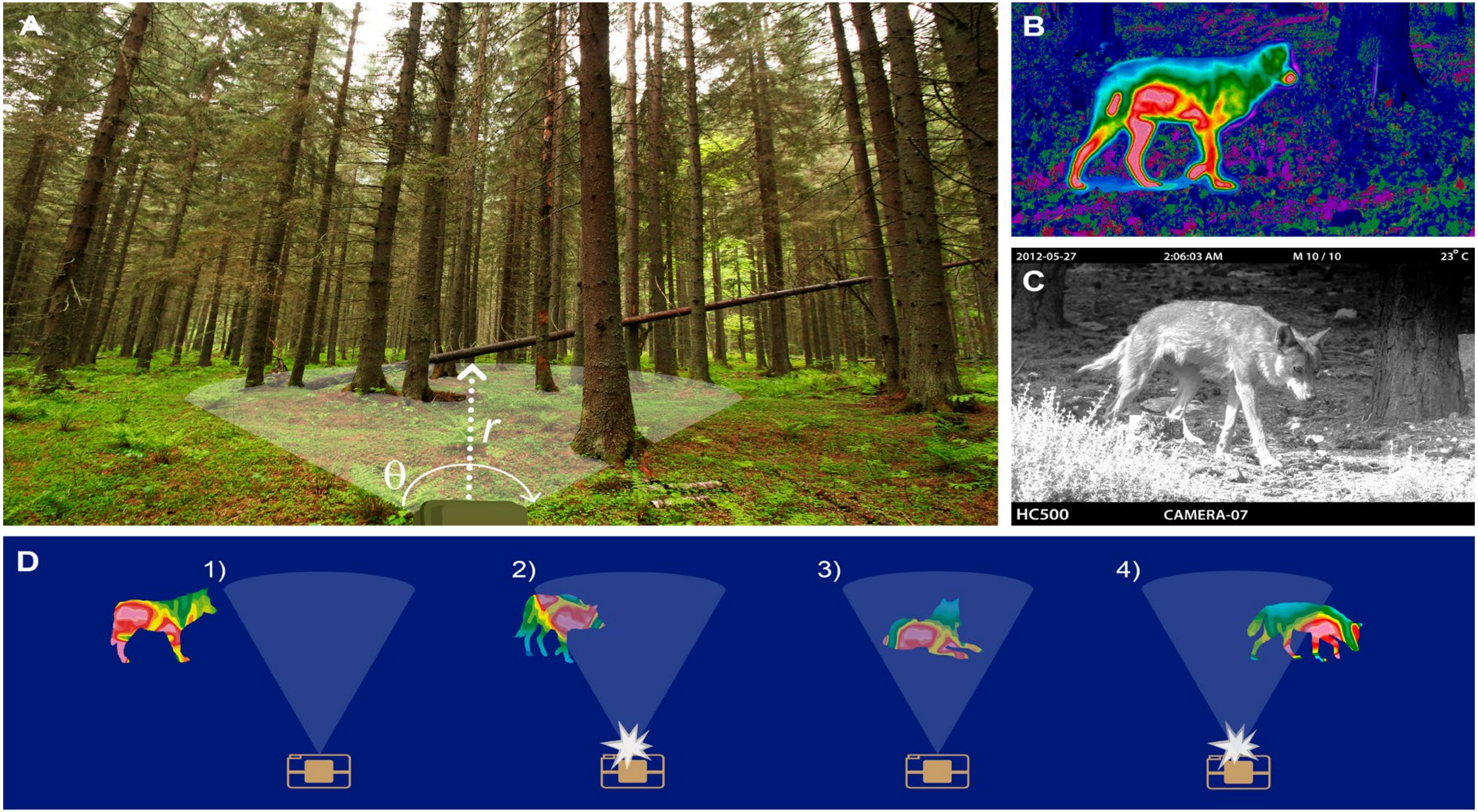


Figure 4-1. How modern commercial camera traps work. Camera traps have a notional detection zone, defined by the radius, r and angle, θ (**A**). Camera traps effectively monitor the surface temperature of the scene inside the detection zone, and warm-blooded animals (here, a wolf) typically stand out from the background (**B**). It is not sufficient for an object to just have a different temperature to the background, but also that they are moving (**C**); this combination triggers the camera trap, including the infrared flash if ambient lighting is poor (producing a black-and-white image of the wolf). An animal will only trigger the camera if it is moving inside the detection zone (**D, 2** and 4); an immobile resting animal (3) may not trigger the camera. Note that, in reality, the detection zone is typically composed of multiple smaller zones (**Box 4-1**), and will vary in size over space and time, and for different species.

BOX 4-1: HOW DO PASSIVE INFRARED (PIR) SENSORS DETECT ANIMALS?

Many researchers, and even experienced camera-trappers, misunderstand exactly how PIR sensors function (Welbourne *et al.* 2016), and this can be detrimental to the success of a camera-trapping study. For example, you may read or hear that PIR sensors detect differences between the ambient air temperature and the animal's body temperature, or you may hear that PIR sensors only detect "heat in motion". Both of these are poor descriptions of how PIR sensors actually work.

PIR sensors are actually composed of two main components which act together: **a pyroelectric sensor and** one or more **Fresnel lenses.** The pyroelectric sensor, in turn, is **composed of two pyroelectric elements side-by-side.** These elements contain a crystal substance which is altered at the atomic level by infrared radiation (i.e. heat) and generates a voltage. All objects with a temperature greater than absolute zero emit some infrared radiation, and the hotter an object is the more infrared it emits. Objects will also reflect infrared, just like objects can reflect light, and some objects reflect infrared better than others. A PIR sensor is "passive" in that the pyroelectric sensor inside it merely detects incoming infrared radiation, and does not generate any radiation itself. In addition, they cannot "see through" objects and are only capable of detecting the **surface heat** of objects infront of them. This means that objects can easily be hidden from view, for example behind vegetation or an uneven ground surface. It also means that the internal temperature of an object is not important (e.g. an animal's core body temperature), and it is the external surface temperature that matters.

If the two elements in the pyroelectric sensor are at a different temperature, then their voltages will differ and an electric current will therefore flow between them. In a normal background scene, the amount of infrared radiation received by the two elements is always likely to differ, due to variation in the amount of heat emitted or reflected by different objects in the scene (e.g. leaves versus tree bark). The important thing, however, is that the size of this initial **temperature difference** (as reflected in the size of the electric current that is flowing) can be noted by the sensor and then monitored over time. If the temperature difference then changes suddenly, this is a good indication that an object (such as animal) is moving across the scene. If the change is above some **threshold,** then a signal can be sent to trigger the camera trap to take an image or video. The threshold can be varied to adjust the sensitivity of the sensor, with lower thresholds resulting in higher sensitivity at the cost of more false triggers. Note that it is the difference in temperature detected by the two pyroelectric elements that is monitored. This means that changes in the surface temperature across the whole scene, as might happen during the course of a day as the sun rises higher in the sky, will be ignored by the sensor. It also means that cold objects in motion will be detected just as well as hot objects in motion.

The Fresnel lenses are used to focus infrared radiation coming from specific directions onto the pyroelectric sensor. This is just like how a camera's lens is used to focus light onto an image sensor. Without a lens, infrared radiation from any direction could hit the pyroelectric sensor anywhere, giving a fuzzy sense of the scene. Multiple Fresnel lenses are used in most camera traps, in order to monitor multiple small areas of a scene for animals. This means that, rather than a single homogeneous detection cone (as the detection zone is characterised in **Fig. 4-1**), **a camera trap's detection zone is usually made of multiple narrow cones,** each covering a specific part of the scene and with gaps in-between. This makes PIR sensors much more sensitive to even small amounts of motion, provided the motion occurs within one of the narrow cones covered by a Fresnel lens. At the same time, this sensitivity to small amounts of motion can make them susceptible to moving vegetation and other inanimate sources of "infrared radiation in motion". These false triggers are a common, if often misunderstood, cause of complaint when using camera traps.

Further reading:
Welbourne *et al.* (2016) give a full account of how passive infrared sensors work, specifically for ecologists.

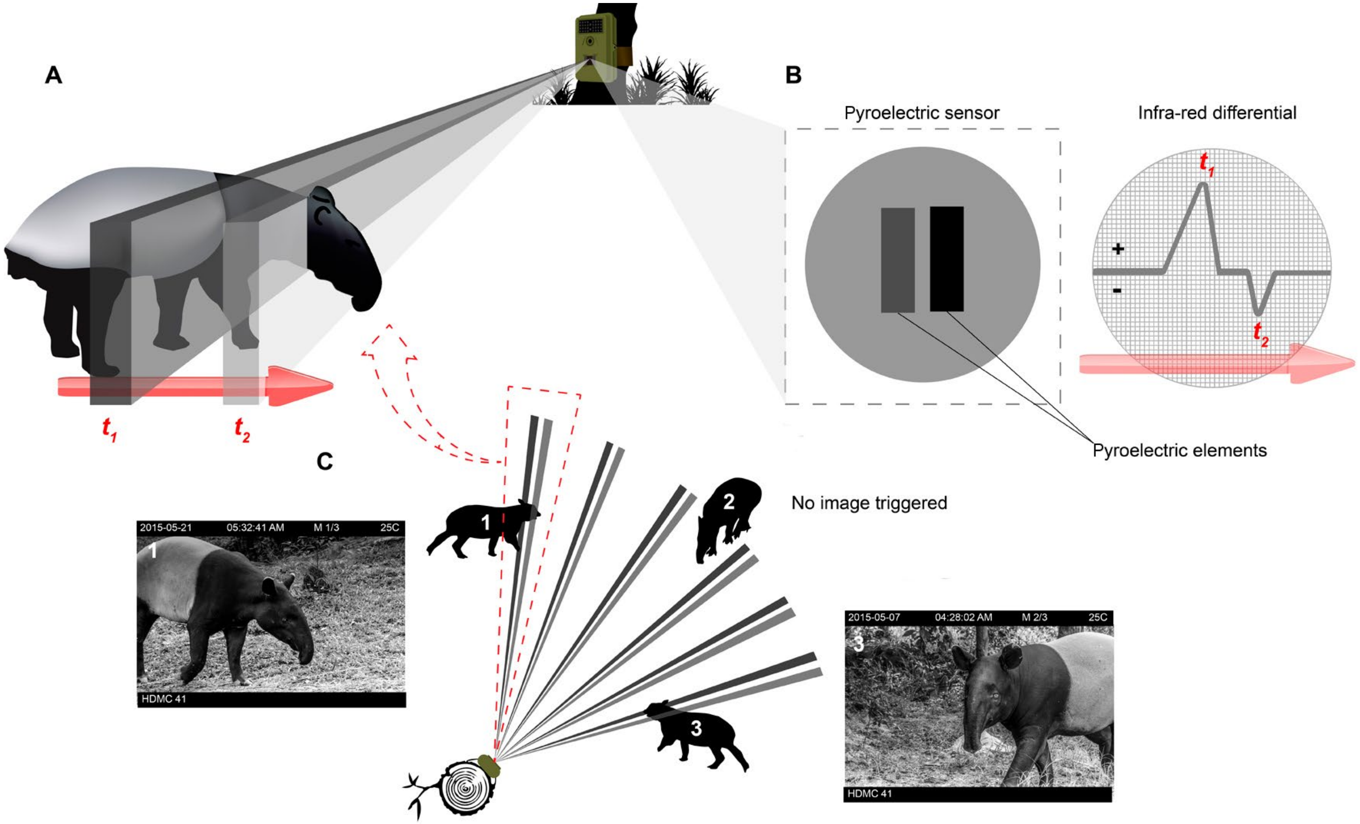


Figure 4-2. How a passive infrared sensor works. The detection zone of the modern camera trap is composed of one or more detection windows. As an animal moves across a detection window (**A**), this causes the pyroelectric sensor to register a difference in the amount of infrared radiation received by the two elements (**B**). If this differential is greater than a certain threshold, an image is triggered. Most camera traps have multiple detection windows (**C**), as determined by the structure of the Fresnel lens. This lens lies over the sensor and focuses infrared radiation from different directions onto the pyroelectric elements. Here, a camera trap is shown with six detection windows (C). Some camera traps may have upper and lower sets of detection windows (not shown here), the latter being used to detect animals close to the camera. Animals that approach a camera trap straight on (e.g. C-2) will often fail to be registered by the sensor, as they may fall between detection windows, or may not generate a differential between the pyroelectric elements.

4-1-2 How do camera traps adapt to different lighting conditions and subjects?

Camera traps don't always yield good photographic results (for example dark, blurry, or out-of-focus images), and an understanding of the basic principles of photography, and how camera traps apply them, can be helpful in trouble-shooting what has gone wrong.

The modern camera trap functions much like a "point-and-shoot" compact camera. For example, camera traps monitor ambient light levels using a day/night sensor (**Fig. 4-3)** and, on this basis, will decide: 1) the **sensitivity** required of the image sensor (ISO), 2) the f-stop and shutter speed to use, and 3) whether to use the **flash**. ISO determines the image sensor gain, and increased sensitivity comes at the cost of increasing noise or "graininess" in the picture. The f-stop determines the relative size of the camera's aperture (the pupil which allows light onto the image sensor) when the image is exposed, and larger aperture sizes allow more light in but come at the cost of decreased depth of field (the depth in the image which will be in focus). Shutter speed is the length of time that the aperture is open when the image is exposed, and slower shutter speeds allow more light in but come at the cost of more noticeable motion blur in the image. When a camera trap is triggered, the optimal settings to obtain a nicely-exposed image are chosen in an instant, based on the manufacturer's software algorithms. Although some cameras (such as Reconyx) allow the user to adjust the weighting given to each of these settings (e.g. by setting the camera to "fast shutter", to reduce motion blur at the cost of exposure), it is often not possible to fine-tune the settings to the exact needs of a given deployment. For this, it is necessary to use a custom DSLR camera trap, on which all of the settings are fully programmable.

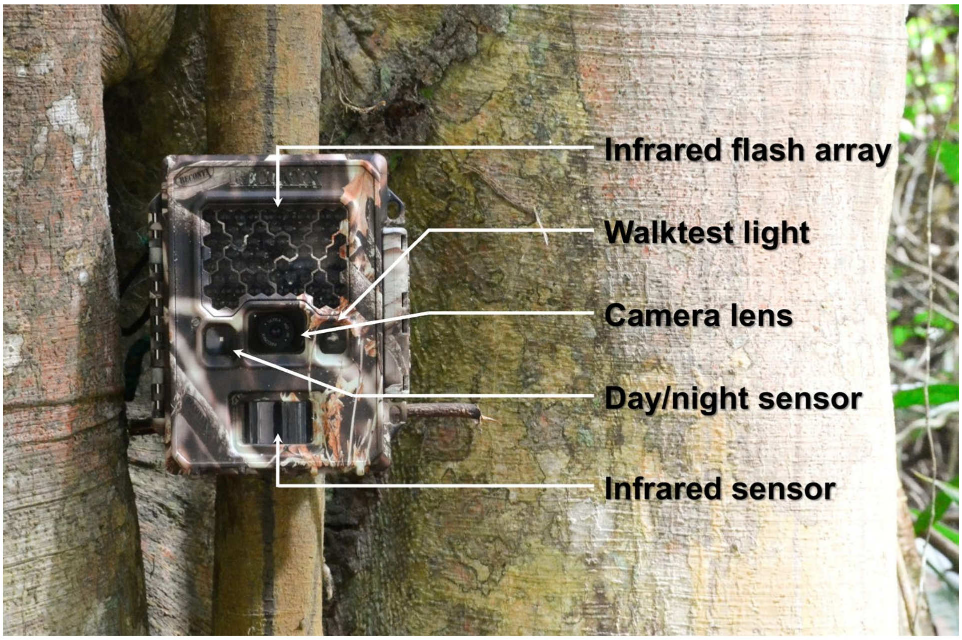


Figure 4-3. The key components of the modern commercial camera trap (Reconyx HC500 shown). The flash array helps produce a properly exposed image in poor lighting conditions. It fires automatically when the day/night sensor receives insufficient light. The walk test light is activated when the camera is set to a testing mode and flashes each time the infrared sensor has registered a detection. This can help the user properly aim the sensor in the field. All of the components of the camera trap are housed within a weather-resistant and camouflaged casing.

Many camera traps use an **infrared flash**, since infrared is invisible to most animals (**see Chapter 4-2-2**). This is possible because standard image sensors (e.g. charge-coupled devices or CCDs) can detect some parts of the infrared spectrum (i.e. the near-infrared range, between 700 and 1000 nm) just beyond the visible light range (390-700 nm). However, image sensors typically have a filter over them (an "infrared cut-off filter" or "hot mirror") to block infrared, otherwise it interferes with the image hue (making them appear pinkish) and contrast (reducing contrast). Most camera traps get around this problem by having a **servo-controlled filter,** which can flip in and out of position as required. This often results in an audible click when the camera takes the first well-lit image at dawn, and the first night image after dusk. Other camera traps just have two separate sensors side-by-side (e.g. Reconyx Ultrafire), which has the benefit of being silent. The images produced using infrared are monochrome (black-and-white), because infrared only activates the red channel in the image sensor (red light has a similar wavelength to near-infrared).

You may also notice in camera trap images that sometimes the animal is sharp, showing all of the fine details on its face and body, whilst in other images it may be slightly blurry and apparently shot in low resolution, even if it is standing still. This is determined by **the focus of the lens** when the image is taken. As with the exposure settings, some camera traps are capable of making a snap decision about where the subject of the image is and focusing on it, but sometimes they will get it wrong, or the animal may be too close to the camera to allow it to be focussed on. Many commercial camera traps instead use a fixed focus (e.g. at 3 m from the camera) combined with a large depth of field. Helpfully, digital camera traps, as with compact cameras, use small image sensors and this means that the depth of field achievable is much larger than in a DSLR. This minimises the chances that the animal will be out of focus in the image. For custom DSLR camera traps, the f-stop can be controlled, allowing for a large depth of field, but at great cost of reduced light levels when the image is exposed. Instead, DSLR camera trap users typically decide where the animal might be on triggering and manually set the focus beforehand to that depth.

4-1-3 The detection zone

The modern commercial camera trap has a **notional detection zone,** in which animals will be detected by the passive infrared sensor. In reality, this detection zone has a complicated structure, usually being composed of multiple detection windows, each in turn composed of two parts (**Box 4.1**, **Fig 4.2**). However, we can usefully approximate it using the simple 2D shape of a cone (technically called a sector), as done under the random encounter model (**Chapter 6-4-4**). This notional detection zone has just two parameters, the **radius**, r and **angle**, θ (**Fig. 4-1**).

When we reduce the detection zone to this simple 2D shape, we can talk about factors that might affect its radius and angle. Most obviously, different camera trap models show large variation in the radii and angles of their detection zones. Manufacturers rarely report these parameters in their specifications and, if they do, they do not divulge how they calculated them. One way of measuring them is to walk repeatedly in front of a camera trap at different distances and record when the camera registers detections. The commercial website Trailcampro.com has done this for many camera trap models, reporting that radii can vary between 10 and 30 m, whilst angles can vary between 15 and 75° (Meek *et al.* 2012). Combining these to calculate the areas covered by the detection zones, shows that they **can differ by an order of magnitude** between models (between 30 and > 300 m2).

However, we probably shouldn't think of the detection zone parameters of a given camera trap as fixed. The parameters reported by Trailcampro.com, for example, have been measured in ideal conditions (a flat surface and open environment, with temperate weather conditions) and with human subjects.
We know that the detection zone parameters will **depend on a whole host of factors,** broadly separated into 1) the **environmental conditions** at a camera trap location and 2) the **characteristics of animals.**

The environmental conditions at a camera trap location that may affect the detection zones will include: how dense the **vegetation** is (and how much of it is cleared during setup); how **uneven** the surface is, and the **microclimatic conditions.** Differences in vegetation density across forest plots in the Netherlands were found to have a substantial impact on detection radii, being 20% lower in closed versus open habitats (Hofmeester *et al.* 2017). Microclimatic conditions, such as ambient temperature and amount of shade, will have an impact on the ability of a passive infrared sensor to detect animals. For example, higher ambient temperatures will usually mean that the surface temperatures of the background scene will be more similar to the surface temperature of animals, meaning that they have to be closer to the sensor in order to trigger it. **Environmental conditions can also vary over time,** as well as over space. For example, for reasons that remain unclear, it was found that detection zone radii on Barro Colorado Island, Panama, were 70% higher in the dry season compared to the wet season, whilst the angles were lower (Rowcliffe *et al.* 2011).

The detection zone parameters can also be expected to vary considerably across species. Most importantly, **species vary in their infrared emissions,** for example due to variation in surface temperatures, the distribution of insulating fur or feathers across their bodies, and their overall body size. Ectothermic species may show little contrast in surface temperature compared to their surroundings, lowering the effectiveness of passive infrared sensors and making detection zones very small (or non-existent). In addition, some species may show little contrast at certain times, such as otters when they are wet (Kuhn & Meyer 2009), meaning that they will likely have to be closer to the sensor to register a detection. However, **body size** has been found to have the most important effect on detection zones, with larger species being detected at larger distances and wider angles (Rowcliffe *et al.* 2011; Hofmeester *et al.* 2017). Very small species (< 100 g) are sometimes detected by higher-end camera traps on the market today (e.g. **Fig 4-3**), but detections will only be reliable at distances less than 2 m from the camera (Rowcliffe *et al.* 2011). There is also some evidence that detection angles are smaller for species which move at **faster speeds** (Rowcliffe *et al.* 2011). Small species which routinely move at fast speeds, such as stoats and weasels, are likely to have especially small detection zones (Glen *et al.* 2013).

Variation in detection zones within a study can be accounted for by explicitly **modelling the radius and angle parameters,** as done under the random encounter model (**Chapter 6-4-4**). Alternatively, the overall effect of varying detection zones on detection probabilities can be modelled (e.g. a higher detection probability in habitat X than habitat Y, due to a more open environment and flatter ground surfaces in X), as done under occupancy and capture-recapture modelling (**Chapters 6-5** and **6-3-2**, respectively).

4-2 Features of the modern camera trap

There are myriad ways in which camera trap models can differ (summarised in **Table 4-1**), but here we examine three of the main distinctions in more detail: full-frame versus compact image sensors; white versus infrared flashes, and networked versus autonomous camera traps.

4-2-1 Compact versus "full-frame" image sensors

All modern digital camera traps bought "off-the-shelf" have image sensors much like those in compact cameras. These sensors are much **smaller in size than the original 35 mm film** that they replaced, typically ~30 times smaller, and produce low- to medium-quality images (although this is rapidly improving). However, the small size of the image sensors, and the smaller size of the lenses used for focussing, allows for increased miniaturisation of the camera housing, so that cameras are more portable and less conspicuous in the field.

DSLR cameras have image sensors that are similar in size to the original 35 mm film (so-called "full-frame" cameras), or slightly smaller (~60% smaller, as in "APS-C" format cameras). Larger sensors, in general, produce much better images, in terms of their visible resolution and perceived quality (**Fig 4-4**). However, they also require larger housings to hold the sensors, and bulky lenses for focussing. No camera trap manufacturers currently produce DSLR-type camera traps with a full-frame (or nearly so) sensor, and no DSLR camera manufacturers provide kits specifically for converting a DSLR into a camera trap. As a result, significant additional time and expense is necessary to put together a bespoke setup that works, and DSLR-type camera traps remain the preserve of professional photographers and enthusiasts.

4-2-2 White versus infrared flash

The early commercial camera traps were all equipped with white flashes, which allow for full-colour images, with little or no motion blur, to be taken in low light conditions (**Fig 4-5**). Although many camera trap manufacturers still produce one or two camera trap models with white flashes, many consumers now prefer infrared flash cameras and these are now more common on the commercial market. This is because of the perceived **downsides of white flash cameras,** in terms of the disturbance they can cause to normal patterns of animal behaviour and movement, as well as the increased conspicuousness of white flash cameras at night to potential thieves. White flashes today come in two forms: **Xenon white flash** and **white LED flash.** Xenon white flashes work by passing a current between two electrodes inside a glass tube filled with Xenon gas. The gas ionizes and emits a very short burst of white light. This "flash tube" technology has been standard in flash photography for decades. More recently, LEDs which produce white light have become a viable alternative to the flash tube. The benefits include better **energy efficiency,** meaning batteries last longer, and no need for recovery between flash events, meaning they can be kept on to record video at night (in contrast to Xenon flashes, which fire once and often then need > 30 seconds to recycle). LED flashes are also silent, unlike flash tubes, which usually emit some noise when triggered. However, current white LED flashes on camera traps are not as powerful as Xenon flashes, reducing effective detection distances and increasing the chances of motion blur. Although there is lots of anecdotal evidence that **white flash can disturb animals** (e.g. Schipper 2007), the extent to which this biases inferences based on camera trap data has been poorly explored. In a capture-recapture study of tigers using Xenon flash, a significant decrease in tiger trapping rates was seen, and this effect materialised rapidly, within the first 5 days of the study (Wegge *et al.* 2004). Modelling confirmed a behavioural "trap-shy" response by tigers, inferred to be due to the white flash (Wegge *et al.* 2004). Similar "trap-shy" responses by tigers have been seen in other studies using white flash (e.g. Sharma *et al.* 2010).

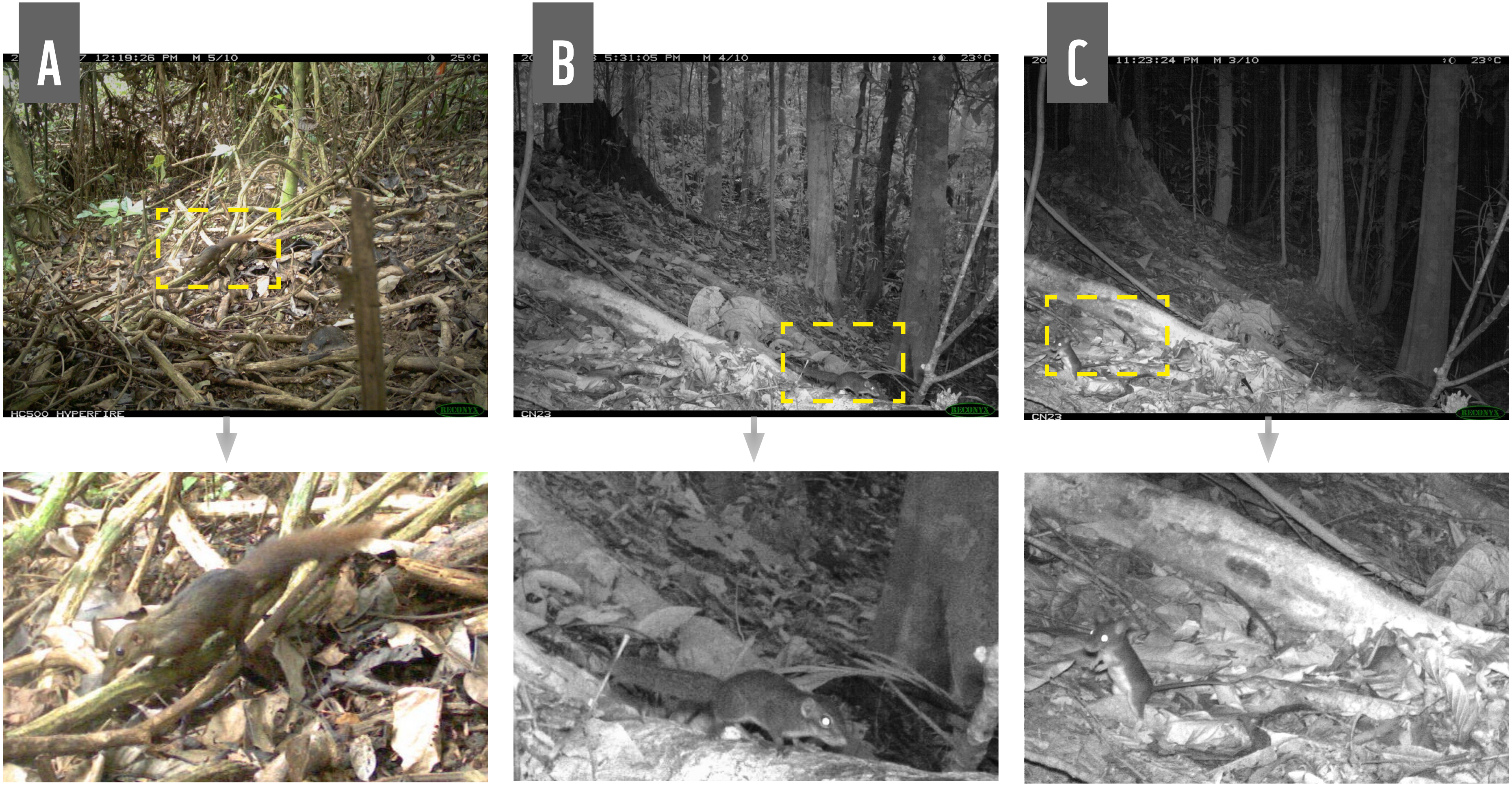


Figure 4-4. Detecting Bornean small mammals with camera traps: large tree shrew, *Tupaia tana*, at ~180 g (**A**), Low's squirrel, *Sundasciurus lowii*, at ~85 g (**B**), and juvenile brown spiny rat, *Maxomys rajah,* at ~70 g (**C**). Example images are from Reconyx HC500 camera traps.

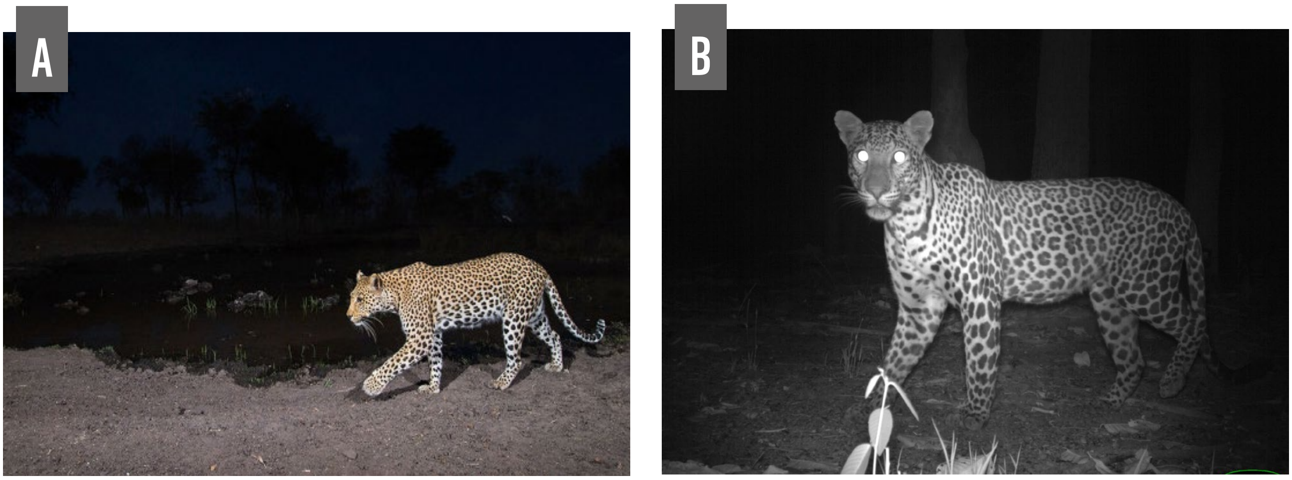


Figure 4-5. Custom DSLR camera trap setups provide the highest quality images. Example images of leopards taken at night using a DSLR camera trap image (**A**) and Reconyx PC900 commercial camera trap (**B**). For the DSLR image, multiple white flashes were used to light the scene, whereas the image from the commercial camera trap was lit using the onboard infrared flash array. The DSLR image is much larger (it contains many more pixels) and can be enlarged and printed at larger sizes than the Reconyx image, without any deterioration. Also note the superior aesthetic qualities of the DSLR image – this is partly to do with the better lighting setup, but also the image resolution and correct focus depth (set manually for the DSLR and automatically for the Reconyx camera trap). Images © Will Burrard-Lucas and © GDANCP/WWF-Cambodia, respectively.

Figure 4-6. White flash is often preferred for capture-recapture studies. Xenon white flash (**A**) is very effective at freezing any movement and more often yields a clear image of the pelage markings. Images taken under infrared flash (**B**), apart from being black-and-white, often suffer from motion blur, which can make it difficult to identify individuals from their pelage markings. Example images of Indochinese clouded leopards (*Neofelis nebulosa*) taken at night using a Panthera v4 camera trap with a Xenon white flash and a Reconyx HC500 camera trap with a near-infrared flash. Images © Sahil Nijhawan/Panthera/APFD.

Infrared flashes use LEDs which emit energy in the **infrared** or **near-infrared** range. This technique takes advantage of the sensitivity of image sensors to infrared, and works by bouncing infrared off animals (and other objects) in order to illuminate the scene, instead of using visible light. This is not the same as thermal or "passive infrared" imagery, which instead uses the infrared emitted from warm-blooded animals to visualise them. This infrared energy emitted by animals is at a much higher wavelength as it is primarily due to heat. The key benefit of using an infrared flash is that, like us, **most animals cannot see infrared,** so they are not disturbed by the flash. Notable exceptions are vampire bats, some snakes and various insect groups (Campbell *et al.* 2002), but these are rarely the targets of camera-trapping. Infrared flash, like white LED flash, can also be kept on to record videos at night, and it is silent (Newbold & King 2009). The downsides of using infrared flash are that they can only produce **black-and-white images,** and they are **not as powerful as white flashes** (especially Xenon flash), meaning that images may be poorly exposed (perhaps only exposing an area very close to the camera) or subject to motion blur. In addition, near-infrared flashes (which emit energy with a peak wavelength of ~850 nm) are not completely invisible to animals (e.g. Newbold & King 2009; Meek *et al.* 2014b), including humans, and for this reason are sometimes called "low glow" flashes, as opposed to "black flash" or "no-glow" flash (~950 nm peak wavelength). The latter is usually more expensive, but can be even more prone to poor exposure and motion blur.

It is worth noting that visualising scenes using infrared can sometimes mask or emphasise details, compared to the same scene visualised using visible light. For example, contrasts in colour on the pelages of animals, which are clear under visible light, can be masked in infrared, making species identification more difficult (**Fig. 4-7**). In some cases, however, infrared can aid identification, as was found to be the case for melanistic leopards, *Panthera pardus*; the characteristic rosette patterns usually remain hidden under natural light, but are much more visible under infrared (Hedges *et al.* 2015; **Fig. 4-8**).

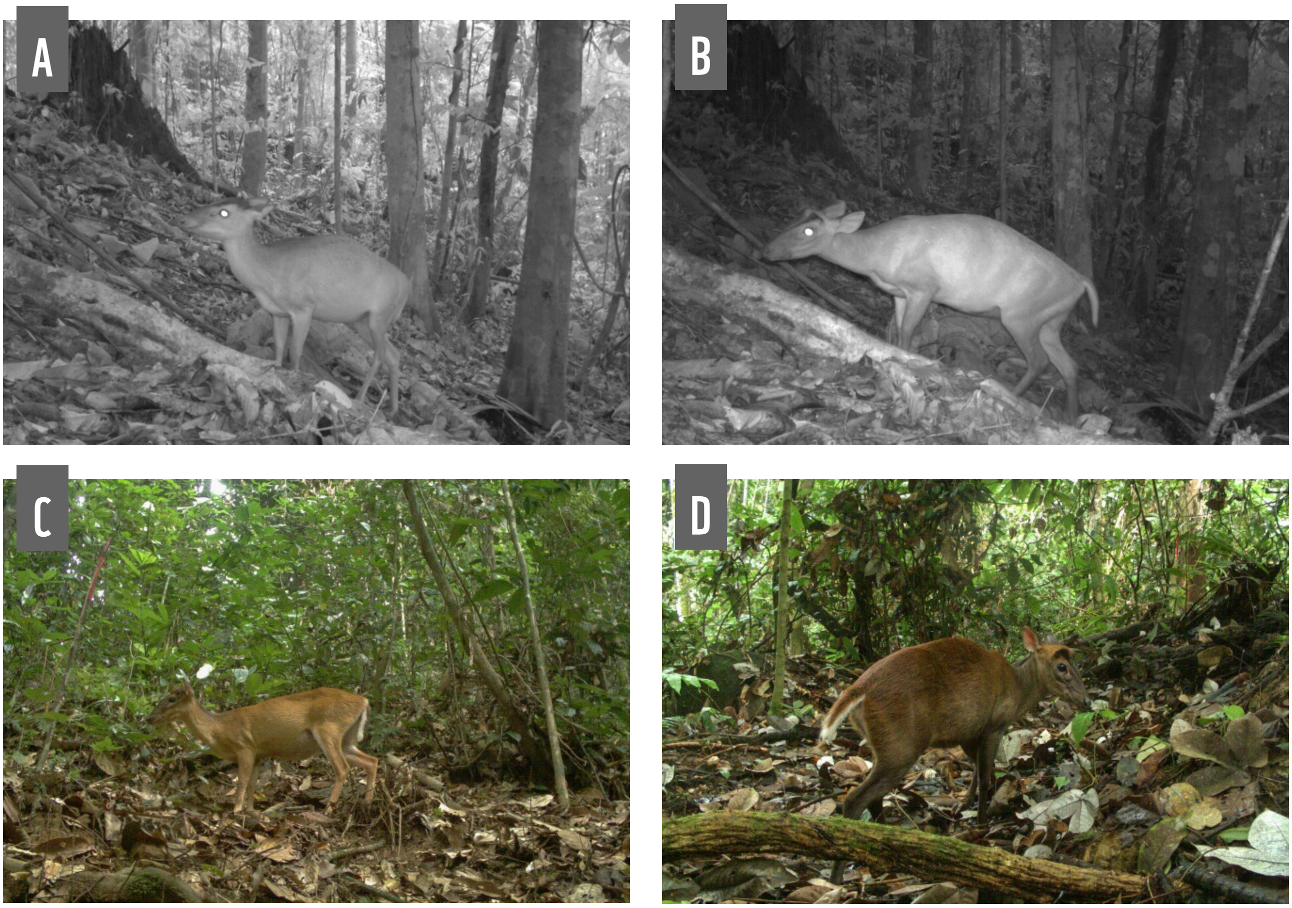


Figure 4-7. Cryptic muntjac species in the forests of Borneo. Under infrared, the yellow muntjac, *Muntiacus atherodes* (**A**) and red muntjac, *Muntiacus muntjak* (**B**) can be difficult to distinguish. However, under natural light or white flash the darker pelage and blackish legs of the red muntjac are clearly apparent (**C** and **D** are yellow and red muntjac, respectively). Example images taken using Reconyx HC500 camera traps with a near-infrared flash.

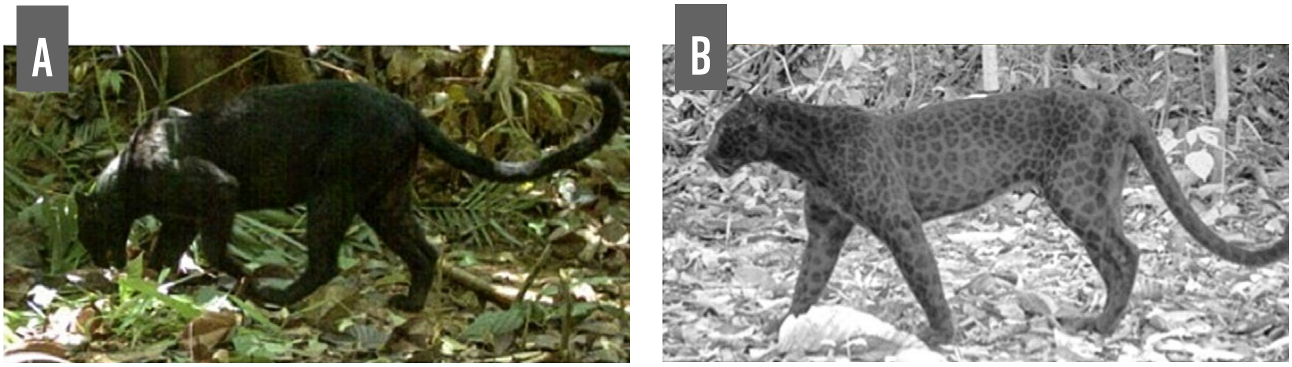


Figure 4-8. Infrared light causes the leopard to reveal its spots. The melanistic population of leopards in Peninsular Malaysia appears all black under natural light (**A**), but the characteristic rosette patterns are clearly revealed under infrared light (**B**). Example images taken during the day using Reconyx HC500 camera traps. Images © Laurie Hedges/Rimba.

Xenon white flash	LED white flash	Near-infrared ("low glow") flash	Infrared ("no glow") flash
			
Colour images	Colour images	Black-and-white images	Black-and-white images
Flash emits a sound and is highly visible; very likely to disturb animals	Flash is highly visible; likely to disturb animals	Flash is weakly visible as a red glow from some angles; will disturb some animals	Flash is almost invisible; will not disturb most animals
Flash is strong and illuminates a large area; animals close to the camera may be over-exposed and difficult to identify	Flash is weaker than Xenon, illuminating a smaller area	Flash strength depends on the camera trap model, but is usually moderately strong, illuminating an area similar to a white LED flash	Weakest type of flash, illuminating a smaller area than a near-infrared flash; compensating by using a slower shutter speed will increase the chances of motion blur
Flash stays on for a small fraction of a second, preventing motion blur	Flash stays on for much longer than Xenon (e.g. 1 second); motion blur will be apparent if animals are moving	Similar to LED white flash, may suffer from motion blur	Motion blur may be even worse than for near-infrared flash
Slow recovery times because the flash needs to recharge	Fast recovery times are possible, because LEDs can be instantly re-fired	As for LED white flash	As for LED white flash
Video is not possible using the flash	Video is possible using LED white flash, although a sustained white light is likely to cause considerable disturbance to animals	Video is possible using near-infrared flash (although typically of shorter durations than during the day, to conserve battery life)	Video is possible using infrared flash, but videos may be quite dark compared to using near-infrared
Flash consumes a lot of battery	LED flash is more energy-efficient than Xenon	As for LED white flash	As for LED white flash

Table 4-1. A comparison of the four major types of flash found on modern commercial camera traps.

4-2-3 Autonomous versus networked camera traps

In the vast majority of cases, it is not logistically or economically possible to check camera traps every day, and a best-guess has to be made about when a camera will need servicing, to replenish batteries or free up some memory. Mismatches between when a camera is checked and when it has actually stopped working are a major cause for **inefficiency in camera trap surveys.** In addition, camera traps have traditionally not provided data in **real time.** This means that any management responses to information they are gathering are delayed, and there is an increased risk of data loss, for example due to theft. To increase the efficiency of camera trap surveys, and provide data in near real-time, camera traps must be networked in some way. A number of camera trap manufacturers have recognised a demand for networked cameras in recent years and have started to produce models which can transmit data over **mobile phone** or **Wi-Fi networks.** The shift from autonomous to networked cameras is likely to increase in the near future, as mobile phone and Wi-Fi networks expand across the globe. Indeed, it may be the case that future camera traps will have relatively limited onboard memory, sending data instead to the cloud for storage. For now, most networked cameras also function as standard autonomous cameras in the absence of a network connection.

Camera traps which can transmit data over mobile phone networks, often called "cellular" cameras, potentially allow for very long-distance communications, for example **sending images to mobile phones, e-mail accounts, or a manufacturer's website.** Data is transferred in near real-time (typically with a short delay, or in bulk at a scheduled time of day), which is especially useful for anti-poaching and security purposes. Some also allow for remote checks to be made, for example of remaining battery life and memory capacity, and even the changing of camera settings remotely.

However, cellular camera traps are subject to many of the same constraints we are used to when using mobile phones. Since they make use of the same technology as our mobile phones, they must be able to communicate with a nearby fixed-location transceiver, such as a radio mast. Although much of the inhabited surface of the Earth is now covered by cellular networks, many of the locations that camera traps are specifically aimed towards are in remote locations without signal. In addition, cellular camera traps **require a strong connection** (ideally 3G and above, with three "bars" of signal), since they are transmitting a much larger amount of data than just voice calls or text messages. They are also much more **expensive** than autonomous camera traps, and require a SIM card and data plan for each camera. An additional consideration is that cellular camera traps are currently **targeted towards the North American market,** reflecting the importance of the hunting market in this region, and therefore compatibility with SIM card providers in other parts of the world is unlikely to have been tested before. Some cellular cameras come with a pre-installed SIM card for the US or Canada which cannot be changed.

Cellular cameras can have very **long recovery times** (> 1 min), whilst they send data over the cellular network. Some cellular cameras have a "batch" transmission mode to circumvent this, but are typically unable to record new images for a period of minutes whilst they are sending data. Finally, cellular cameras typically send **low-resolution copies of the images** and no videos; the memory cards need to be retrieved for the full-resolution originals.

Wi-Fi camera traps, also sometimes called “wireless” camera traps, use high-frequency radio waves to transmit data over **short and medium distances** (< 1 km). Wi-Fi camera traps typically communicate with a dedicated **base-station,** which collects data from nearby networked cameras and stores it in a single location for later retrieval. If the camera trap has a “line of sight” view of the base-station, transmission distances of 300-500m are possible, but this depends on the terrain and habitat (e.g. dense forest will attenuate the signal much more than open habitats, and even small hills will completely block signals). **Distances of less than 100 m are more typical** in field conditions. In some systems (e.g. the Buckeye long-range wireless system), each camera trap can also act as a repeater for other camera traps in the network, passing images along a “daisy chain” and allowing much greater transmission distances in the process. Cameras can also be equipped with high gain Yagi antennas to extend transmission distances. Even over relatively short distances, Wi-Fi camera traps may offer substantial benefits over autonomous camera traps. Depending on the accessibility of the base station, Wi-Fi camera traps may allow for near real-time data transfer (if, for example, the base station is in a research station or ranger outpost) and for status checks to be made in an instant. Camera settings can also be changed dynamically in this case. Some manufacturers, such as Buckeye, are experimenting with cellular-equipped base-stations, but the low bandwidth offered by mobile phone networks is especially challenging in this case. Even if the base station is not networked and cannot be readily checked, it can still serve as a **data back-up,** reducing the chances of data loss due to camera theft or destruction. Some Wi-Fi camera traps also allow communication with smart phones or computers in the field. This may be particularly useful for arboreal camera traps, enabling status checks to be made from the ground, instead of having to use laborious canopy access techniques each time.

The downsides of Wi-Fi camera traps are of course the short range of data transmission, as well as the **high power consumption** used by Wi-Fi chips, which greatly shortens battery life. As with cellular cameras, data transmission is typically limited to **low-resolution images** and can **slow down recovery times** (to > 30 seconds) or, in batch transmission mode, mean that the camera is out of action for a short period of time.

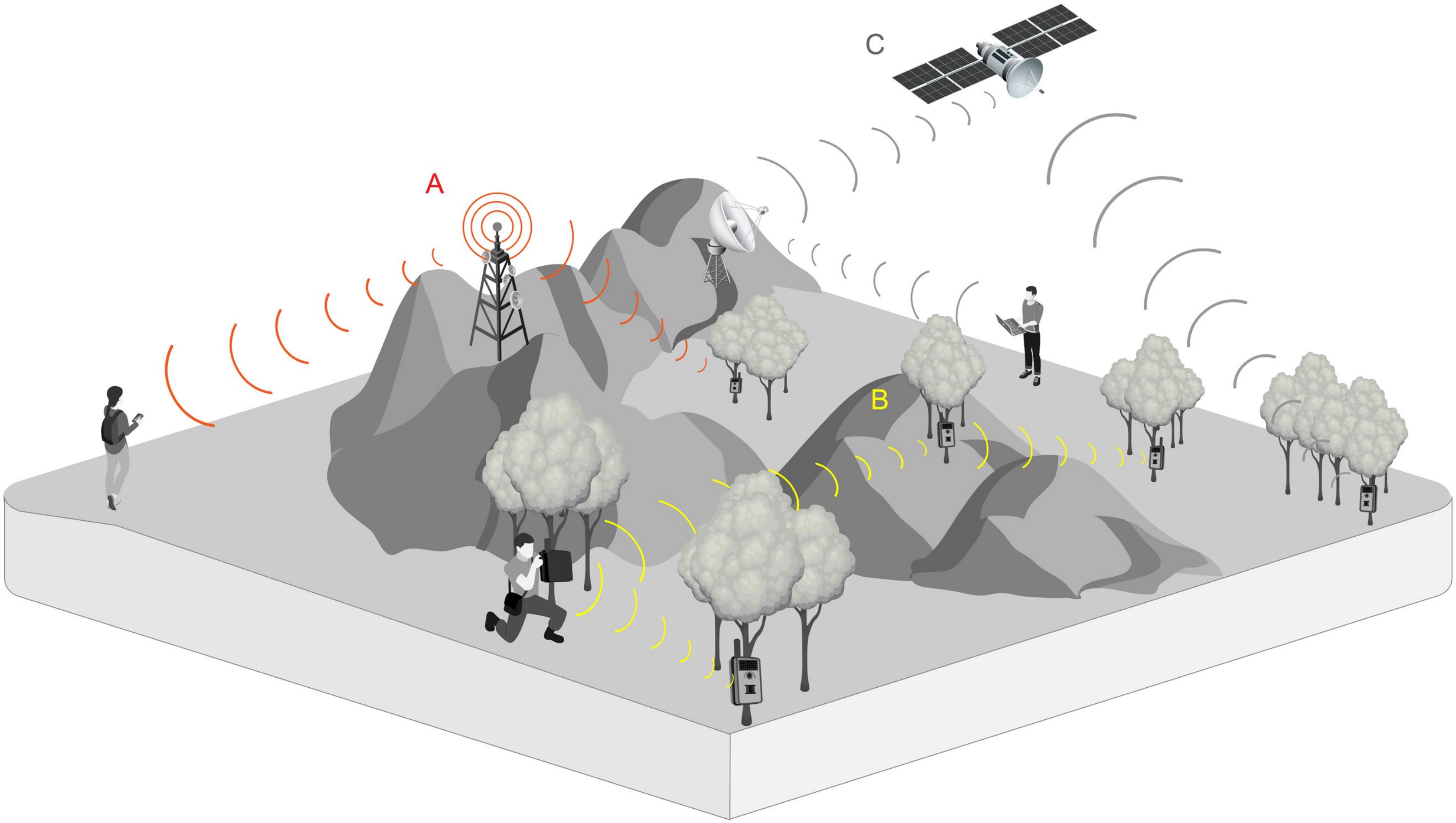


Figure 4-9. Networked camera traps allow for more efficient data collection and the remote transmission of data in near real-time. “Cellular” camera traps connect to mobile phone networks and allow camera trap images to be sent to mobile phones or e-mail accounts, but cameras must be within range of a cellular mast (**A**). Wi-Fi camera traps connect over a local network to a central base station, which securely stores the images in an accessible location until they are manually retrieved (**B**). Transmission distances for Wi-Fi camera traps can be extended using strategically-positioned “repeater” camera traps (such as on a hill-top). In areas with no mobile or Wi-Fi networks, it is technically possible for camera traps to send images over satellite phone networks (**C**), but this remains prohibitively expensive and offers only limited bandwidth.

4-2-4 Other features of camera traps

Feature		Options	Key considerations
Cost		\$50 to > \$1000	Cost varies from cheap, poorly-manufactured units at the low end, to bespoke DSLR setups with multiple flashes. Cost is often of primary concern, but beware "false economies", i.e. buying poorly-performing cameras in bulk, when a smaller set of high-quality and suitable units would have been more effective. First identify the camera features you require and then consider the cost you will have to budget for.
Trigger	Trigger type	Direct or indirect	Indirect triggers, such as passive infrared sensors, are highly effective and sample across a broad-range of species. They are the default option. Direct triggers (such as active infrared sensors or mechanical systems) should be considered where indirect triggers fail or are not selective enough.
	Trigger speed	0.1 to 4 seconds	How fast a camera responds to a detection and records an image, i.e. the trigger speed, is a key parameter to take into consideration. Slow trigger speeds (> 1 s) will miss faster-moving animals and will function poorly along trails (where animals will often be walking quickly across the field of view).
	Recovery time	0.5 to 60 seconds	The time it takes for a camera to recover from an initial trigger and re-trigger for a second time, i.e. the recovery time, is important if multiple captures of animals are required. Multiple captures can help with counting animal group sizes and to identify individuals or species. Slow recovery times can also mean that interesting behaviour is missed.
Detection zone	Detection distance	Reported as 10 to 30 m	As for trigger speed, the size of the detection zone is a key parameter to take into consideration. The detection zone effectively determines the area that has been sampled and, summed over all of your cameras, can have a big impact on the amount of data that is obtained. The maximum distance that a sensor can detect a target, i.e. the detection distance, helps to determine the size of this detection zone. Importantly, this detection distance will vary depending on the size of the animal, so reported distances must be taken in a relative sense. For close-up work, or in dense vegetation, the detection distance may be of lesser importance.
	Detection angle	Reported as 15° to 75°	Along with detection distance, the detection angle determines the size of the detection zone, and therefore can have a big impact on sample sizes. The detection angle will vary depending on the size of the animal and the speed at which it enters the detection zone, so reported figures must be taken in a relative sense. As for detection distance, wide detection angles may be less important for close-up work, or in dense vegetation. Note also that detection angles larger than the field of view angle (typically 40°) may be of limited value and may lead to blank images.
Image sensor	Imaging method	Film or digital	All modern camera traps have image sensors, the digital equivalent of the film used in the first camera traps. Image sensors are of two broad types – "charge-coupled devices" (CCD) or "complementary metal-oxide semiconductor" (CMOS) - with similar end results. CMOS sensors have gradually replaced CCDs in digital cameras, and are used in many of the new off-the-shelf camera traps. Although the first digital camera traps had very slow trigger and recovery times, they are now mostly faster than film camera traps. The principal advantage of digital imagery is that the number of images that a single camera trap can take, without servicing, is order of magnitudes higher than with film. There is now no reason to prefer film over digital camera traps.

Feature		Options	Key considerations
	Image sensor size	Full-frame or compact	A DSLR camera trap will have a much larger image sensor than an off-the-shelf camera trap. Some DSLRs have “full-frame” sensors, equivalent in size to 35 mm film, or they may have sensors a bit smaller than this (e.g. “APS-C” sensors, which are about half the size). Off-the-shelf camera traps use the same technology found in compact cameras, and use sensors ~30 times smaller in area than 35 mm film. In general, larger sensors can contain a) more pixels, leading to higher resolution images, and-or b) larger pixels, leading to less noisy and better exposed images. These factors will improve the perceived “quality” of the image (e.g. for artistic purposes), and make it easier to identify individuals and species. However, constant technological advances mean that there is no simple relationship between the size of a sensor and image quality.
Imaging capabilities	Resolution	Reported as 2 to 20 megapixels	The visible resolution of an image is, in part, determined by the pixel resolution of the sensor. However, beware paying too much attention to the number of “megapixels” quoted by camera manufacturers. Many cameras “scale up” images using interpolation algorithms, so that a “14 MP” camera is actually 3.1 or 5 MP natively. The visible resolution of an image is also determined by the signal-to-noise ratio of the sensor and the quality of the lens. Poor image exposure, motion blur and poor focus will also limit the visible resolution. Pay more attention to other features of the camera, such as trigger speed and the detection zone. If truly high resolution images are required, then a custom DSLR camera trap must be used.
	Images per trigger	1 to 10	Some cameras offer a “burst” mode, in which multiple images are taken in quick succession after each trigger. As with quick recovery times, this can be useful for obtaining multiple images of an animal, aiding identification of individuals and species, and the counting of group size. If the camera takes pictures fast enough (> 1 frames per second), a “near-video” effect is achieved, which can record the movements and behaviour of animals.
	Media types	Images or video (or both)	Many camera traps can now record video (often with sound) as well as images. Some take an image first, and then record a video straight after. Videos can be useful for outreach, because they are more captivating than images alone. They can also record subtle behaviours in detail. However, videos have much larger file sizes, are more difficult to process, and usually involve slower trigger and recovery times compared to images. Battery life is also considerably shorter when using video. Serious consideration should be given to these issues; “near-video” may often be a better compromise for research purposes.
	Time-lapse		Some cameras can be programmed to take a picture at regular intervals, either instead of or in addition to being triggered by animals. This can be a last resort option in cases where triggering is ineffective. Setting a camera to take a picture each day can also be useful for later determining exactly how many days it was functioning for.
	Programmable schedule	Can be set to operate only during certain hours or days, or always on	A programmable schedule can be useful for targeted deployments for specific species (e.g. noctural species) and to reduce unwanted images (e.g. of people during the day).

Feature	Options	Key considerations
Field of view	35° to 100°	The horizontal extent of a scene that is visible in images, i.e. the field of view (FOV), is largely determined by the focal length of the camera lens. In other words, a large FOV is achieved by "zooming out" from a scene, whilst "zooming in" will result in a smaller FOV. Wide-angle lenses allow a large area to be seen in images, but animals will be much smaller in the frame. In addition, a wide FOV is often not matched by a similarly wide detection angle, reducing its usefulness. Most camera traps have a "standard" FOV (~42°). Telephoto lenses have a narrower FOV and can be useful for capturing a small target in the distance, but the trigger must be highly specific (e.g. an active infrared sensor) otherwise lots of blank images will be taken. Finally, fish-eye lenses (up to 180° FOV) can be fitted on DSLR camera traps, but the image distortion is considerable on these lenses and may make identification difficult.
Flash type	Xenon, white LED or infrared LED	The type of flash a camera uses has a large bearing on its usefulness for different tasks. Xenon white flashes (i.e. "flash tubes") and white LED flashes produce colour night-time images, whilst infrared LED flashes produce monochrome images. This can have a large impact on the ability to identify species, some of which may have diagnostic colours. In addition, LED flashes are not as strong as Xenon flashes, and often result in motion blur if the target animal is moving fast. This may cause problems for species identification and for identifying individuals from their markings. However, white flashes can alter behaviour and lead to animals becoming "camera shy". Infrared flashes, on the other hand, are invisible to most animals and are now the default option.
Battery life	Days to months	Battery life depends on the efficiency of the camera when it is in standby mode, how much energy it uses when taking images/videos (including using any flashes) and its battery capacity. Most camera traps are powered by AA batteries, and the battery capacity is affected by the number of batteries used (typically 8 or 12), as well as the type of battery used (alkaline, nickel metal hydride or lithium). In addition, battery life will be affected by external factors, such as the number of images or videos that are taken each day and the temperature (lithium batteries are relatively unaffected by temperature). As a result of all of these factors, it is difficult to estimate how long a camera will run for, but all things being equal a lower resting current draw (measured in milliwatts, mW) will mean longer battery lives. Some cameras are also compatible with external power sources, such as large lead-acid batteries or solar panels. Most off-the-shelf cameras can run for weeks or months, whilst DSLRs and other home-brew setups are often limited to days.
Connectivity	Cellular or Wi-Fi	Networked camera traps are able to transmit data over mobile phone or Wi-Fi networks. Cellular cameras send images to a mobile phone, e-mail address or website platform. This means that data from cameras can be received in near real-time and the current status of the camera can be checked. Some cellular cameras also allow the user to change settings remotely. Wi-Fi camera traps instead send their images to a central base station, which can then serve as a single focal point for retrieving data, as well as a back-up in case of camera loss. If the base station is highly accessible (such as in a field station), it can also allow for data to be viewed in near real-time and camera settings to be changed dynamically. Networked cameras are still very much experimental, and can perform poorly or fail altogether. For example, they depend on a strong network signal, data can fail to send if lots of images are taken in succession, and recovery times can be poor. Moreover, transmitted images are typically low-resolution copies (cameras must be visited in-person to retrieve the original images) and videos cannot be sent.

Feature		Options	Key considerations
Housing	Size and weight		Although there is a general trend towards smaller and lighter camera traps, there is still considerable variation among models. This can have a large impact on how portable they are, and the labour costs of deploying them in remote areas. In addition, smaller cameras can be deployed more discretely, and can have a lower risk of theft/vandalism. Active infrared setups, and especially DSLR camera traps, consist of multiple parts and can be bulky to transport.
	Resistance to animal attack		Most cameras are housed in strong plastic shells which are impenetrable to most animals, but some cameras can have protruding or removable parts which are susceptible to being broken. The strength of the closure mechanism can also determine whether an animal can break open a camera. If the camera housing has any small holes in it, or weak points such as humidity vents, then ants and termites can enter and damage the circuitry. Some animals are very hard to guard against (such as elephants, bears and hyenas) and replacement cameras must be budgeted for in such cases.
	Waterproofing		Fully waterproof cameras should be sealed, with rubber gaskets around any openings. This is essential to stop any ingress during heavy rain.
Humidity protection			Humid environments, such as tropical rainforests, are not friendly towards electronics, and corrosion can occur on circuit boards and battery connections in a matter of weeks. Some cameras come with a conformal coating on the circuit board which protects it from humidity. In addition, some manufacturers encourage consumers to deploy silica-gel drying agents inside the camera, and have provided spaces for this in the design.
Security	Lockable case		Cases with padlock loops allow the batteries and memory card to be more safely secured inside the camera, deterring opportunistic thieves (and animals).
	Security cases and locks		Some manufacturers offer optional security cases, designed to fit around their camera traps. Third-party manufacturers also offer cases for more popular camera trap models. These metal cases offer additional protection from wildlife and vandalism, as well as securely protecting the batteries and memory card. Many cameras are now designed to be compatible with cable locks, to securely attach cameras to trees or posts.
	Camouflage		Camouflaged housing can help to conceal cameras from thieves/vandals, if the design is appropriate to the deployment environment.

Feature		Options	Key considerations
Manufacturing	Quality and consistency		As for most consumer electronics, cheaper units offer suffer from lower manufacturing quality and consistency. This may cause units to malfunction or fail earlier than expected. For example, cameras made in the USA tend to be more reliable than those made in Asia (primarily China), but considerably more expensive.
Ease-of-use	Mounting options	Screw mount, camera mount, cable or strap	Camera traps with a tripod thread can easily be attached to a screw mount on a tripod or dedicated camera trap mount. Tripods may be useful where there are no other attachment options, such as in open areas, whilst camera mounts can be useful for vertical or angled deployments of cameras (e.g. in tree canopies or for monitoring small mammals from above). Most cameras are designed to be attached to objects using straps and bungees. A more secure option is to use cable locks, but not all cameras are compatible.
	Setup aids	Testing mode or “live-view”	During camera setup, it can be useful to have feedback on whether the infrared sensor is properly aligned and is unobstructed. Many commercial camera traps have a testing (“walk test”) mode, in which a light on the front of the camera trap flashes to indicate if a detection would have been registered. Other cameras offer a “live-view” mode on an external device to make sure the images will be correctly composed.
	Programming and documentation		Programming the settings should be a simple, intuitive and logical process, which can reduce human error. In addition, English-language instructions can reduce misunderstandings about how specific camera traps function.
	Media playback	In-built screen or separate device for viewing	Many cameras have built-in screens for immediately reviewing images and videos. This can be useful during testing in the field, or for other instances when immediate playback is beneficial. Otherwise, separate devices (smart phones, tablets or laptops) must be used to review images in the field.
Customer support	Reputation and warranty		Some manufacturers have a good reputation for providing technical support and offering repairs or exchanges at low or no cost. In addition, they may offer a warranty to cover units which malfunction due to poor workmanship or faulty components.

Table 4-2. The many dimensions along which camera traps can differ, including in each case the options available and the key points to understand.

4-3 Broad types of camera trap

Although camera traps vary along lots of dimensions, they tend to cluster into one of a few restricted types (**Table 4-3**). This lack of diversity is a function of the relatively small market for camera traps, and the overwhelming dominance of the recreational hunter market, which demands a relatively narrow set of characteristics from camera traps. As a result, most camera traps are simply passive infrared sensors connected to a compact digital camera, with an infrared flash. This suits the hunting market. Within that, there are budget cameras (usually < $250, made in China, and offering very little customer support), and more expensive mid- to high-end cameras with better detection circuitry and overall reliability. A small number of manufacturers are also producing more unusual camera traps, that may be networked or have unusual detection circuitry or lenses. Finally, hobbyists and professional photographers are frequently devising their own customised setups, by repurposing (i.e. "hacking") other equipment or assembling a bespoke system from commercially-available parts.

Type of camera trap	Typical features	Typical use-cases	Example manufacturers
Custom	DSLR or re-purposed compact camera; often triggered with an active infrared sensor or other direct trigger; custom lenses and white flashes used for artistic effect; expensive; limited battery life; difficult to setup and maintain, so typically only deployed in very small numbers	Behavioural studies (e.g. nest monitoring); herpetological studies; wildlife photography (including high-speed)	Faunatech; Phototrap; Pixcontroller; Canon/ Nikon setups with active or passive sensors (e.g. Camtraptions, Eltima, Jama, TrailMaster etc.)
Budget (usually < $250)	Triggered using a passive infrared sensor; poor detection capabilities (e.g. slow trigger speed); can be difficult to setup; variable build quality and operating life; cheap and able to be deployed in larger numbers, with mixed results	Inventory work; community outreach and education	Bolymedia; Ltl Acorn; Scoutguard
Mid- to high-end (usually $300-700)	Triggered using a passive infrared sensor; consistent and highly effective detection capabilities (e.g. fast trigger speed and large detection zone); consistent quality control; warranty and good customer support; deployed in lower numbers due to greater cost, but with consistent results	Research and monitoring work (diversity, occupancy, abundance/ density)	Bushnell; Cuddeback; Reconyx
Experimental	Triggered using a passive infrared sensor; may be networked (Wi-Fi or cellular); may have an unconventional lens (such as macro or wide-angle); may allow for an external power source; expensive; largely untested and should only be deployed at scale after extensive testing	Behavioural studies; anti-poaching	Buckeye; Moultrie; Spypoint; Uway; some manufacturers also have "experimental" models

Table 4-3. Broad types of camera trap at the disposal of researchers and conservationists, varying from cheap off-the-shelf units, to high-quality customised setups.

Camera traps provide a window onto wildlife populations, relatively free of the disturbances caused by other sampling methods. At the same time, they produce permanent and verifiable records of animals, akin to traditional museum voucher specimens.

Image of southern pig-tailed macaques, *Macaca nemestrina*, grooming: © Oliver Wearn

5 THE CAMERA TRAP'S NICHE

HIGHLIGHTS

- Camera traps are good at recording hyper-rare events and offer the chance to make observations with minimal disturbance
- Camera traps were initially used mostly in studies of avian behaviour and ecology, but are today mostly used in monitoring the abundance and distribution of large mammals
- The captivating images and videos that camera traps produce also makes them effective public engagement and educational tools, for example as part of citizen-science programmes
- Most recently, camera traps are being employed as surveillance tools in protected areas, in particular to combat poaching
- Camera traps bring many benefits: they sample for long periods of time; are relatively non-invasive; can record undisturbed behaviour; produce verifiable data, and offer a highly-repeatable method of data collection
- The drawbacks to camera traps include: their large upfront costs; sometimes poor performance in extreme environments; their vulnerability to interference from humans or wildlife, and their focus on a relatively narrow subset of biodiversity (medium-to-large, warm-blooded and terrestrial animals)
- Published studies have shown that, in a wide variety of cases, camera traps often out-perform other sampling methods (yielding more detections, and of a wider variety of species), and are especially cost-efficient when used for long-term monitoring

Camera traps are the most patient and focussed field workers you will ever have, willing to quietly sit in one spot waiting for events to unfold in front of them. They excel, in particular, at recording so-called **"long tail" events** (named after the "long tail" of a frequency distribution), such as a top predator passing by, or the predation of a bird's nest. In addition, they attempt to circumvent the "Heisenberg effect", in which the observation of a system can alter its state. Camera traps mostly do not disturb the events they witness, and allow for the recording of relatively **natural behaviours.** These key benefits of camera traps – recording of hyper-rare events, without disturbing wildlife – have meant that camera traps have proven to be useful in a wide variety of ways (**Table 5-3**).

5-1 What have camera traps been used for?

5-1-1 Past uses of camera traps – 1950-1990

Cutler & Swann (1999), in the first review of studies using remote cameras, found that early camera traps (often large, and triggered mechanically) were already being used to study a variety of topics. They placed the studies they found (published between 1956 and 1997) into six categories according to their primary topic of interest: 1) **nest predation** (32% of camera trap studies); 2) **feeding ecology** (25%); 3) temporal and spatial activity patterns (16%); 4) presence of a species (11%); 5) nesting behaviour (10%), and 6) population parameters (6%). In addition Cutler & Swann (1999) noted that the majority of studies were concerned with **birds** (62% of studies using remote cameras, i.e. including time-lapse cameras).

Figure 5-1. Nest monitoring with camera traps. Before 1990, camera traps were primarily used to study birds, primarily in monitoring nests. Here, a camera trap is being used to monitor a saker falcon (*Falco cherrug*) nest in Hungary. Image © János Bagyura.

5-1-2 Current uses of camera traps – 1990 to today

The topics identified by Cutler & Swann (1999) all remain relevant today, but there has been a substantial shift in how camera traps are primarily used, and in the taxonomic groups studied. This followed Ullas Karanth's proof-of-concept applying **capture-recapture analysis** to camera trap data (Karanth 1995; Karanth & Nichols 1998), as well as a substantial **reduction in the size and cost** of camera traps, meaning that camera traps could be deployed in large numbers over large areas. As a result, there was a rapid rise in the number of camera trap studies that focussed on **monitoring animal abundance,** particularly of terrestrial mammals (McCallum 2013). This was followed shortly after by a similar rise in the number of camera trap studies focussing on species distributions, again of terrestrial mammals, and in particular using the **occupancy methods** advocated by Daryl Mackenzie and colleagues (MacKenzie *et al.* 2002, 2006).

Burton *et al* (2015) reviewed the most recent camera-trapping literature (2008-2013), finding that **most studies were of population parameters** (relative abundance and density), followed by species presence, animal behaviour, and occupancy. In addition, **95% of studies focussed on mammals** – in particular carnivores (65% of studies) – and just 12% of studies included birds (Burton *et al.* 2015).

"Eyes on Leuser"
www.eyes-on-leuser.com

HabitatID
www.habitatid.org

Naturespy
www.naturespy.org

Snapshot Serengeti
www.snapshotserengeti.org

eMammal
www.emammal.si.edu

As well as the camera trap's well-established role in studying and monitoring wildlife, they are now becoming increasingly used in **public engagement** and **education** programmes. For example, a number of initiatives have used camera trap images and videos to build local and international support for protected and unprotected areas. Camera traps can produce highly captivating and candid images of species or behaviours that even people local to an area might never have seen. In Southeast Asia, this approach was used by the "Eyes on Leuser" project in Sumatra, Indonesia, and by HabitatID in neglected protected areas in Cambodia and Thailand. Aside from the images produced by camera traps, the technology itself can be a vehicle for engaging local communities with the wild landscapes that surround them. In the UK, the "Wild North Wales" project, run by the non-profit organisation Naturespy, deployed camera traps in parks and reserves with the help of local community groups, educating local people about camera traps and the wildlife that exists in their area. Camera traps have also been fundamental to a number of large-scale **citizen-science** projects in recent years, including the "Snapshot Serengeti" project on the Zooniverse online platform, as well as various projects run through the Smithsonian Institute's "eMammal" platform.

ZSL InstantDetect
www.zsl.org/conservation-initiatives/conservation-technology/instant-detect

Camera traps are also now being used as covert and inexpensive **surveillance** tools (e.g. Hossain *et al.* 2016). Previously, there were few cheap options for surveillance in remote areas, but camera traps are changing that. Conservation organisations, such as WWF, Panthera and the Zoological Society of London (ZSL), as well as private land managers, are exploring the use of camera traps as **anti-poaching tools.** For example, ZSL's "InstantDetect" camera trap system aims to detect poachers using a combination of sensors, including acoustic (to detect gun shots), magnetic (to detect metal objects, such as guns) and seismic (to detect vehicles and footfall), and alert relevant authorities in real-time over a satellite network.

Figure 5-2. Camera trap image of a red fox (*Vulpes vulpes*) in central London, UK. Since 1990, there has been a shift in the use of camera traps, towards population monitoring, especially of mammal species such as this fox. Image © Chris Carbone.

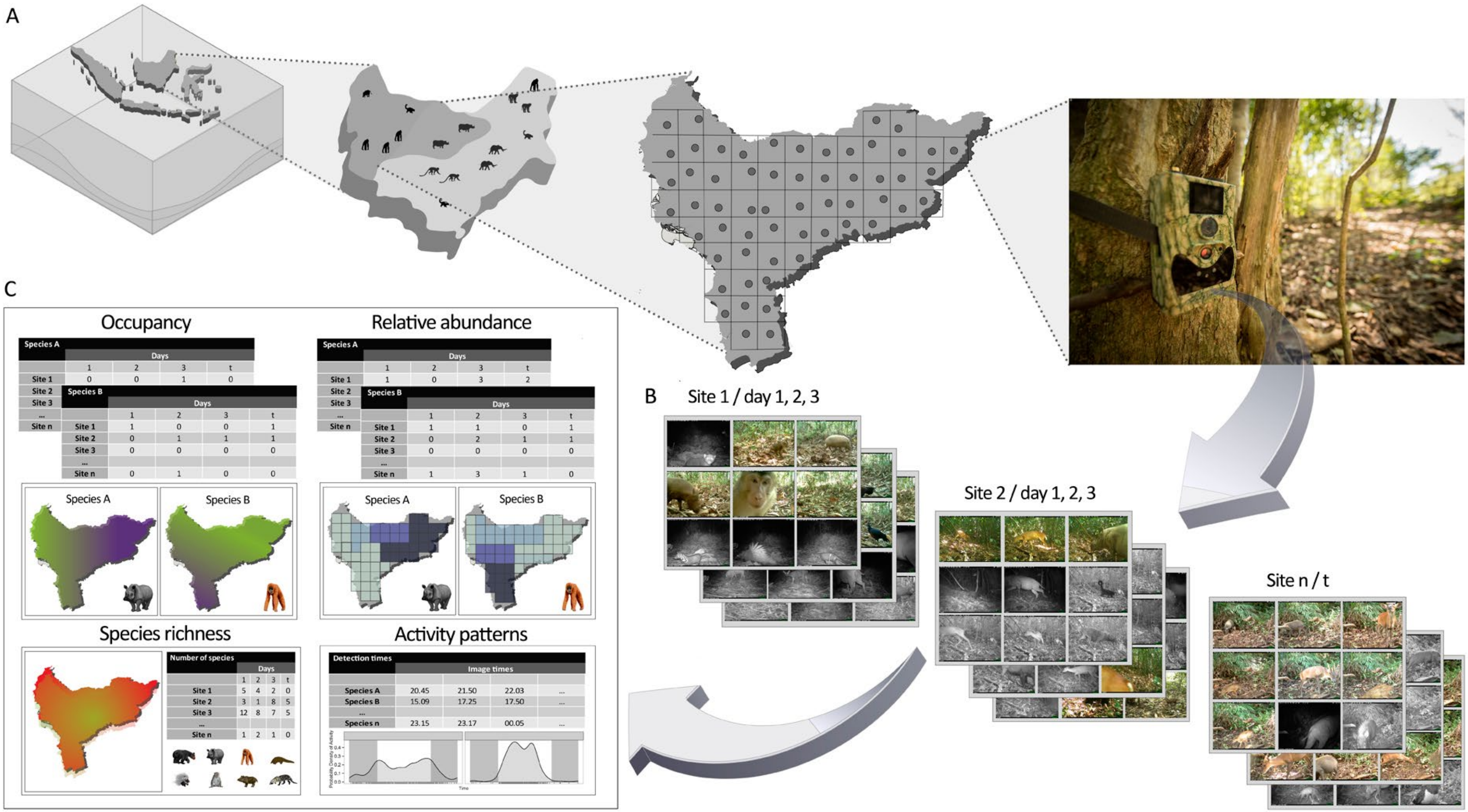


Figure 5-3. The modern large-scale camera trap study. (**A**) The study area is delineated and a grid is overlaid, with camera traps deployed in each grid cell. (**B**) Camera traps collect data at different sites for multiple days. (**C**) This spatial and temporal replication of sampling effort allows the data to be used in multiple ways, including the estimation of occupancy, relative abundance, diversity and activity levels. The approach for a capture-recapture study is different to that shown here (see **Fig. 6-1**). **Chapter 7** of this guide provides detailed recommendations for survey design depending on the specific aims of a study.

Broad research topic	Specific topic examples	Alternative methods available to researchers
1. Species inventory work	Species presences	Direct observations (haphazard sampling); sign surveys; live-traps; track plates; hair traps; acoustic sensors; environmental-DNA sampling; local ecological knowledge; market surveys; museum records; citizen science records
2. Species distribution and occupancy	Species distribution modelling; occupancy	Direct observations (transects, plot searches, hides); sign surveys; live-traps; track plates; hair traps; acoustic sensors; environmental-DNA sampling; local ecological knowledge
3. Population parameters	Relative abundance; density; survival/ recruitment; dispersal	Direct observations (transects, plot searches, hides); sign surveys; live-traps; track plates; hair traps (with DNA sequencing); radio- or GPS-tracking; acoustic sensors
4. Community-level parameters	Species richness/ diversity; β-diversity	Direct observations (transects, plot searches, hides); sign surveys; live-traps; track plates; hair traps; acoustic sensors
5. Animal behaviour	Habitat-use; activity patterns; phenology; foraging and feeding ecology	Direct observations (hides to minimise disturbance of natural behaviour); radio- or GPS-tracking
6. Species interactions	Predation; competition; frugivory and mutualism	Direct observations (hides to minimise disturbance of natural behaviour)
7. Human-wildlife interactions	Hunting; crop-raiding; livestock	Anti-poaching surveys; direct observations; market surveys; social surveys (interviews and questionnaires)

Table 5-1. Broad and specific research topics that can be addressed, at least in part, using camera-trapping methods. Depending on the context, alternative sampling methods available to researchers may be more effective, or cost-efficient, at addressing many of the given research topics.

5-2 The pros and cons of camera traps

Camera traps have found such a large number of uses because of a unique set of advantages they possess over other rival tools. A single camera trap deployed in the field can collect **vast amounts of data**, and over a **very long time period**, relative to many other sampling methods. Thousands of animal detections can be made by a camera trap before it needs servicing by a field worker, compared for example to just a single detection for most live traps, or tens of detections for a track plate. This allows camera traps to record very rare, **"long tail" events.**

Camera traps are considered to be a **"non-invasive" method**, in that although animals may alter their behaviour in response to a camera trap, they do not physically capture or harm animals. Deployed correctly, they allow a window into the **behaviour** of animals relatively undisturbed by humans. They allow researchers to obey the best-practice motto "take only photographs and leave only footprints". This is not to say that there are no impacts of camera traps (Meek *et al.* 2014b, 2016a), but the impacts are much reduced relative to some other sampling methods.

Although camera traps are restricted primarily to medium- and large-sized mammals and birds, they are still a relatively **broad-spectrum sampling** method. Across a range of studies, camera-trapping detected between 60-100% of the medium and large mammal species known to occur at a study site (O'Brien 2010). In addition, camera-trapping can yield data on small mammals, small birds and reptiles. In one study in Borneo, camera traps detected 17 of the 21 species of small mammal known from the area, as well as 30 bird species and 4 large reptile species (Wearn 2015). The total species list from camera traps in this study extended to 95 confirmed species of mammal, bird and reptile (Wearn 2015).

Camera traps are also a highly effective way of sampling **nocturnal species,** which usually make up the majority of mammal communities. These species can be difficult to observe with direct observations, but passive infrared sensors and infrared flashes allow us to "see in the dark" and uncover the natural behaviour of these species, often for the very first time. Since camera traps work around the clock unhindered, they also offer a unique window into the **activity patterns** of a species, which would otherwise require the invasive process of tagging animals, for example with radio collars.

Since camera traps make detections using an electronic sensor, they are a far more **repeatable and replicable** sampling method than some other options, especially those which use humans as detectors. For example, the exact same camera trap model can be deployed by different research teams on opposite sides of the planet. This is exactly what the Tropical Ecology Assessment and Monitoring (TEAM) network is doing (Beaudrot *et al.* 2016), in this case using Reconyx Rapidfire and Hyperfire camera trap models, which all have broadly similar detection characteristics. The relatively simple process by which passive infrared sensors make detections can also be modelled explicitly (Rowcliffe *et al.* 2011), allowing for greater comparability of datasets which have been collected using different camera trap models.

The raw data that camera traps produce acts as a **permanent and verifiable** record of a species or event at a particular time and place. This makes it comparable in many ways to a museum voucher specimen, albeit digital rather than physical. Other methods, such as line transects or track plates, do not yield similarly verifiable data. Of those methods that do, such as trapping or shooting, individuals of the species must be sacrificed. Just like the museum specimens of old, digital specimens from camera traps have led to species **range extensions** (Pettorelli *et al.* 2010; Lhota *et al.* 2012; Samejima & Semiadi 2012; Sastramidjaja *et al.* 2015) and **rediscoveries** (Wilting *et al.* 2010b; Ferreira *et al.* 2014), and have even played a role in discovering **new species** (Rovero & Rathbun 2006).

The benefits of having verifiable data, able to be re-evaluated by a wider scientific community if needed, are especially useful for those species which are difficult to identify (e.g. because they look similar to another species, or because they´re very rarely seen). For example, after a camera trap survey in Borneo, a press release was issued declaring a putative new carnivore species, but on closer inspection by a wider range of experts, this "carnivore" actually turned out to be a relatively common species of flying squirrel (Meijaard *et al.* 2006).

The obvious appeal of using camera traps to sample wildlife communities is the fact that the raw data is so immediately captivating. Camera trap images can be used to **communicate science**, to **raise awareness** and **educate**, and to build support for a species or habitat. The camera-trapping method itself may also be an effective method of engaging local communities in wildlife issues in some circumstances. Camera trap surveys are also proving to be a suitable way of enlisting the help of **citizen scientists** to both collect and process biodiversity data at large scales (McShea *et al.* 2016; Swanson *et al.* 2016).

There are also significant drawbacks to camera traps. The primary drawback is the very large **upfront cost** of the equipment. Mid-range camera traps are $300-500 to buy, and a robust camera trap survey (e.g. involving 50 camera traps) might cost in the region of $15,000-40,000, depending on the specific aims. Although the recurrent labour costs associated with camera traps are low, because they can operate unassisted in the field for long periods, the equipment costs are significantly higher than most other sampling methods. Camera traps also produce large amounts of data, and the labour costs to store and then process all of it, most often manually, can be considerable.

Most **electronic devices perform poorly in extreme environments,** such as high precipitation or humidity, and camera traps are not really exceptions to this rule. Unfortunately, camera traps are not yet as resilient as many first-time users expect them to be, and can **malfunction** or become irrecoverably **damaged** when left outside for long periods (see **Chapter 10-9** for more on the problems caused by certain environments, as well as potential solutions).

If the environment does not take its toll on a camera trap, there is often a good chance that **interference by humans or wildlife** might compromise it instead. Theft and vandalism are major constraints on camera trap studies around the world, causing significant losses of data and equipment. Wildlife, including everything from elephants to ants, is also a major problem in some habitats. No general solution exists for these problems, and in most cases camera traps remain vulnerable when deployed in the field (but see **Chapters 10-5** and **10-6**).

Although camera traps are relatively broad-spectrum in their sampling, **ectothermic and small-bodied animals** remain very challenging, especially using commercial camera traps with passive infrared sensors. Bespoke setups, which can be expensive, are needed in order to sample these types of animals with camera traps (e.g. Welbourne 2013). **Aquatic species** are also currently beyond the realm of most camera-trappers, since passive infrared sensors do not work under water. However, some new approaches that could work under water are being trialled, such as pixel-change detection (e.g. Nazir *et al.* 2017). Currently, the best camera-based option for aquatic species is to use time-lapse imagery or video (e.g. Whitmarsh *et al.* 2016).

Some of these drawbacks will be removed or diminished with **technological advances** in the future. If nothing else, camera trap technology is certain to get better over time, for example leading to better detection capabilities, higher quality images, lower power requirements, and greater resilience to field conditions.

Key benefits of camera traps	Counter-arguments
Once deployed, a camera trap can record very large amounts of data with minimal labour costs	Initial equipment costs for camera traps, batteries and other equipment are very high
Non-invasive sampling, with minimal impacts on wildlife	Cannot obtain physical samples (e.g. DNA or tissue) or biometric measurements
Continuous 24 hour sampling of a broad range of species, especially mammals and birds	Small, ectothermic or aquatic species remain very challenging for camera traps
Camera trap images provide a wealth of other data, for example on behaviour, body condition, activity patterns (from the time stamps), and even local habitat characteristics	Often not possible to identify individuals in camera trap images, in which case ecological insights are gained at the level of a species or whole community
Detections are made with an electronic sensor, reducing human observer biases and increasing the potential for replicability and repeatability	As with all electronic devices, camera traps are prone to malfunctioning or failing in extreme environments, such as high precipitation or humidity
Camera trap images of a species in a particular place at a particular time can serve as a kind of digital specimen, akin to a museum voucher specimen, which is verifiable and can be stored indefinitely	Camera trap data needs to be catalogued and stored, which can be a laborious and expensive process
Camera trap raw data is highly captivating, and can be used to communicate research findings and to raise awareness or support for a cause	Camera traps come with legal and ethical risks if they capture images of people, especially those conducting illegal activities
Camera trap technology is constantly evolving, for example leading to improvements in detection capabilities and image quality	Theft, vandalism and damage from wildlife remain as significant problems in many parts of the world, and technological advances are unlikely to solve this quickly

Table 5-2. Benefits, and associated counter-arguments, to the use of camera traps for research and conservation.

5-3 How do camera traps compare to other sampling methods?

For some purposes, such as observing rare behaviours, the camera trap can often be the only reasonable option. However, for other purposes, such as species inventory work or abundance monitoring, there are a diversity of other methods available (**Table 5-1**), many of which have a longer pedigree than camera-trapping. How does camera-trapping compare to these other methods? The answer appears to be that it compares very favourably (**Table 5-3**).

Camera traps have been compared to a diversity of other sampling methods (e.g. line transects, live traps, track plots and hair traps), and for a range of different aims (e.g. estimating species richness or density), but in most cases they have been judged to be superior (see **Table 5-3** for specific examples). Across comparative studies, camera traps in many cases recorded **more detections** than competing methods (e.g. Rovero & Marshall 2009; Paull *et al.* 2012; Glen *et al.* 2014; Dupuis-Desormeaux *et al.* 2016). Moreover, these detections were **more reliable and richer in information**; species identifications from tracks or faeces can be unreliable (e.g. Mckelvey *et al.* 2006; Harrington *et al.* 2010; Janečka *et al.* 2011), and usually do not provide information on group size, behaviour, or the time and date that species were present. In addition, for those studies that incorporated survey costs, a common pattern was that camera-trapping is an expensive survey method for short one-off surveys, but becomes increasingly **competitive over longer time-frames** (e.g. Lyra-Jorge *et al.* 2008; Ford & Clevenger 2009; Zero *et al.* 2013; Spehar *et al.* 2015; Welbourne *et al.* 2015). Many of these comparative studies used film cameras, or early digital cameras with poor detection characteristics, which makes these findings even more compelling. The competitiveness of camera traps compared to other sampling methods will only continue to increase as technology improves.

Reference	Method compared to camera traps	Metrics	Taxa	Habitat	Conclusions	Camera traps best?
Anile *et al*. (2014)	Scat surveys (with DNA sequencing)	Precision of density estimate, capture probabilities	Wildcat (*Felis silvestris*)	Temperate forest (Italy)	Capture-recapture density estimates from camera traps were more precise than from genetic analysis of scats. Individual capture probabilities were also higher with camera traps. However, genetic analyses revealed the extent of hybridisation with domestic cats, which could not be achieved with camera traps.	Yes
Barea-Azcón *et al*. (2007)	Line transects (for scat), track plots, live-trapping	Species richness, detection rates, costs	Carnivores	Mediterranean shrubland (Spain)	Line transects (for scat) and track plots detected the most species, followed by live- and camera-trapping. Only for 1 of the 6 species (wildcat, Felis silvestris) was camera-trapping relatively effective. Camera trap surveys were also the most expensive method, albeit including the price of live bait (pigeons) in this study.	No
De Bondi *et al*. (2010)	Live-trapping	Detection probabilities, costs	Small mammals	Temperate forest (Australia)	Camera-trapping recorded more species overall, although there was no difference evident at the sampling point level. Detection probabilities did not indicate a clear winner out of camera- and live-trapping. Once costs were incorporated, however, camera traps were clearly more efficient than live traps, due to the higher labour costs associated with the latter.	Yes
Dupuis-Desormeaux *et al*. (2016)	Track plots (made using sandy soil)	Species richness, detection rates	Large mammals	Shrublands and savanna (Kenya)	Camera traps recorded nearly three times the number of species and nearly double the number of detections over the same period. Camera traps also provided a wealth of other data on activity patterns, group sizes and behaviour.	Yes
Ford *et al*. (2010)	Track plots (at wildlife-crossing structures)	Detection rates, costs	Large mammals	Boreal forest (Canada)	Both methods had broadly similar detection rates, but showed significant differences for four species (2 were higher for camera traps, 2 were higher for track plots). Camera traps were more cost-effective for longer surveys (e.g. at least 1 year in length), and provided more reliable species identifications.	Yes

Reference	Method compared to camera traps	Metrics	Taxa	Habitat	Conclusions	Camera traps best?
Janečka *et al*. (2011)	Scat surveys (with DNA sequencing)	Accuracy of density estimate, fieldwork costs	Snow leopard (*Panthera uncia*)	High mountain (Mongolia)	Fieldwork for scat surveys was 50% cheaper than for camera-trapping (equipment and salary costs were not included). However, scat surveys must be carefully designed, or there is a risk of over-estimating abundance. The authors recommend that large-scale monitoring of snow leopards is done using scat surveys.	No
Li *et al*. (2012)	Line transects (signs and direct observations)	Species richness, community composition	Mammals	Temperate forest (China)	Camera traps detected more species than the transects for a similar number of person days, and made more detections of small-sized mammals (< 1 kg). The authors advocate complementing existing line transect surveys being done in the region with camera-trapping.	Yes
Long *et al*. (2007)	Detector dogs (with DNA sequencing), hair traps	Detection probabilities, costs	Black bears (*Ursus americanus*), fishers (*Martes pennanti*), bobcats (*Lynx rufus*)	Temperate forest (USA)	Detector dogs had a much higher detection probability than camera traps for the three species. Hair traps had by far the lowest detection probabilities. Detector dogs were the most expensive method (followed by camera traps and then hair snares), but were the most cost-effective.	No
Lyra-Jorge *et al*. (2008)	Track plots (made using sandy soil)	Species richness, detection rates, community composition, costs	Medium- and large-sized mammals	Cerrado (Brazil)	Both methods detected the same number of species. Track plots yielded higher detection rates, especially of smaller species, but species identification was harder. Camera-trapping was more expensive for a rapid 10 day survey, but cheaper in the long run (30 day survey, or repeated surveys).	Yes
Paull *et al*. (2012)	Hair traps	Species richness, detection probabilities	Small and medium-sized mammals	Temperate forest (Australia)	Camera traps recorded twice the number of species as hair traps overall, and about 10 times the number of species at the sampling point level. Detection probabilities were also much higher for camera traps. Species identification also requires much less training in the case of camera traps.	Yes

Reference	Method compared to camera traps	Metrics	Taxa	Habitat	Conclusions	Camera traps best?
Rovero & Marshall (2009)	Line transects	Number of species recorded, costs	Duikers	Tropical moist forest (Tanzania)	Line transects detected fewer species than camera traps, and only 1 species had > 1 direct observation. Camera traps allowed for easier species identification, and surveys were also cheaper and quicker to conduct.	Yes
Rydell & Russo (2015)	Mist nets	Species richness, detection rates	Bats	Temperate forest (Italy)	The number of species detected was the same for the two methods, with 9 of 11 species detected by both methods. Detection rates were higher for camera traps, and camera-trapping is a minimally invasive method compared to mist-netting. The authors also note that both methods are preferable to acoustic recorders, which can miss some species with faint echolocation calls.	Yes
Silveira *et al*. (2003)	Line transects (signs and direct observations)	Species richness	Medium- and large-sized mammals	Grassland (Brazil)	Line transects detected more species than camera traps after 12 days, but this difference had disappeared by 30 days. The authors favour camera traps overall, due to easier species identification, low recurrent labour costs, and the greater range of data that they provide (e.g. on activity patterns).	Yes
Spehar *et al*. (2015)	Nest counts (in plots)	Precision of density estimate, costs	Bornean orangutan (*Pongo pygmaeus*)	Tropical rainforest (Indonesia)	Camera-trapping (with capture-recapture analysis) produced a more precise density estimate than nest counting, and provided a host of additional information on the population at the same time (e.g. age structure, health and behaviour). Nest counts are substantially cheaper, but camera-trapping would become more competitive with repeat surveys. The authors conclude that camera-trapping represents a promising new tool for estimating primate densities.	Yes

Reference	Method compared to camera traps	Metrics	Taxa	Habitat	Conclusions	Camera traps best?
Trolle *et al*. (2008)	Line transects (direct observations)	Ability to produce density estimate	Lowland tapir (*Tapirus terrestris*)	Pantanal (Brazil)	Line transects (with distance sampling analysis) and camera-trapping (with capture-recapture analysis) produced similar density estimates, although the latter was heavily dependent on assumptions about tapir movements. Even so, the authors recommend camera-trapping in future, because the surveys take less time and are able to provide robust data on other species (e.g. jaguars).	Yes
Welbourne *et al*. 2015	Live-trapping, artificial refuges	Species richness, detection probabilities, costs	Small mammals, squamates	Heathland (Australia)	Camera-trapping (with a drift fence) detected more species than the other methods, and most species had higher detection probabilities over the survey period. Camera traps were more expensive for a single survey, due to high equipment costs, but were projected to be cheaper in the long term.	Yes
Zero *et al*. (2013)	Line transects, digital photography	Precision of density estimate, costs	Grevy's zebra (*Equus grevyi*)	Savanna and tropical dry forest (Kenya)	Digital photography (with capture-recapture analysis) gave the most precise density estimate, followed by camera-trapping (using random encounter modelling) and then line transects. Camera-trapping was the most expensive method for a single survey, due to high equipment costs, but the authors project that it would be the cheapest for long-term monitoring.	Yes (for long-term monitoring)

Camera traps provide data on exactly where species are, what they are doing, and how large their populations are. They can be used to build up a picture of whole communities of species, including how they are structured and how species are interacting over space and time.

Image of a Gobi bear, *Ursus arctos,* in Mongolia: © Nathan Conaboy / ZSL

6

ESTIMATING STATE VARIABLES WITH CAMERA TRAPS

HIGHLIGHTS

- State variables are formal measures which tell us something about the state of a community or population, and camera traps are highly effective tools for their measurement
- Species richness is a simple and widely-used state variable, but it does not consider the evenness of a community since all species are weighted equally
- Species diversity measures incorporate community evenness and align with our notions of what constitutes a "diverse community", but they can be harder to interpret and communicate than simple richness
- Community variance (i.e. β-diversity) is a poorly-appreciated dimension of biodiversity which is important for understanding biodiversity patterns and in the design of wildlife reserves
- Population abundance is simply the number of individuals in a population, but is problematic to estimate using camera trap data because individuals usually can't be distinguished, and because some individuals will be missed by the camera traps ("unseen" individuals)
- Trapping rates are often used as an index of population abundance ("relative abundance indices"), but they are not easy to compare across space, time, studies or different species
- For species in which individuals can be distinguished, including a lot of felid species, abundance can be obtained using capture-recapture methods, which correct for the number of "unseen" individuals
- Other species are only "partially-marked", in that only some individuals are identifiable (e.g. pumas), and in this case abundance can be obtained using mark-resight methods
- For species which cannot be identified in camera trap images (i.e. "unmarked" species), the "Royle-Nichols" model can be used to estimate abundance
- Population abundance estimates make most sense in enclosed habitats (such as fenced reserves or islands), but in continuous habitat it is often unclear what "population" they exactly refer to, making it difficult to compare across studies or different species
- Population density (abundance per unit area) is often considered the "gold-standard" state variable and can be directly compared across space, time, studies and different species, but it requires a lot of effort to estimate
- Capture-recapture and mark-resight abundance estimates can be converted to density by ad-hoc calculation of the effective sampling area covered by a trapping grid
- Versions of capture-recapture and mark-resight also exist which estimate density directly, using the spatial information obtained during a camera trap survey (such as where exactly each individual was captured)
- Random encounter modelling (REM) is a unique approach that also provides density directly; it requires randomised placement of camera traps and the estimation of animal speed and activity levels (among other parameters)
- Occupancy has been proposed as a cheaper alternative to density for monitoring, because it only requires detection and non-detection data; however, it should be remembered that it fundamentally represents a measure of distribution and not abundance

Despite their beginnings in studies of behaviour, camera traps are today most commonly used to conduct ecological assessment and monitoring work, for example to answer the following questions:

- **Which species** are present in a study site?
- How **diverse** are species communities?
- How are species **distributed** across space?
- How **abundant** are species?
- What is the **population health** of a species?
  Are individuals surviving and reproducing?

To rigorously answer each of these questions, it is necessary to formally estimate the value of a **state variable**. A state variable is defined as any one of a set of variables that can be used to describe the current state of a dynamic system, such as a population or even an ecosystem. For studies of wildlife, state variables are usually related to the numbers and spatial distribution of species, and of individuals of a species. State variables can tell us enough about a dynamic system, such as a population, to make **predictions** about how it will respond when conditions change. For example, we might be able to make predictions about how populations will respond to increases in the threats that they face (such as land-use change), or to changes in management (such as protecting habitat). The formal estimation of state variables is important, because it forms a **more defensible and objective** basis for making decisions than using informal data exploration, or just personal opinions, alone.

We now give an overview of the major types of state variable that it is possible to estimate using camera traps and discuss their pros and cons.

6-1 Species richness and diversity

Species richness (the number of species found in an area) is a state variable that has been of interest since the very beginnings of ecology. Darwin, Wallace and von Humboldt all alluded to the broad-scale patterns in species richness we see across latitudinal and elevational gradients. Species richness plays a fundamental role in much of modern ecological theory, and features in one of ecology's few laws, the species-area relationship (Lomolino 2000). Through its role in island biogeography theory (Macarthur & Wilson 1967) and, latterly, in conservation prioritisation schemes (e.g. Myers *et al.* 2000; Wilson *et al.* 2007), it remains prominent in the minds of many wildlife biologists and conservationists. Species richness is **the most common state variable** used to assess and predict the effects of human impacts on biodiversity (Gibson *et al.* 2011; Wearn *et al.* 2012; Newbold *et al.* 2015) and is often used at the local scale in biodiversity monitoring and management (Yoccoz *et al.* 2001). The enduring popularity of species richness as a state variable is partly due it long history of use, but also because it is the simplest possible characterisation of biodiversity and is therefore **easy to interpret and communicate.**

Camera traps lend themselves well to the counting of species, because of their broad-spectrum sampling. Indeed, a large number of camera-trapping studies have used species richness as the state variable of interest. Some studies have used **observed species richness** (e.g. Kitamura *et al.* 2010; Pettorelli *et al.* 2010; Ahumada *et al.* 2011; Samejima *et al.* 2012), which is simply the sum of the number of species seen, whilst others have used various measures of **estimated species richness** (e.g. Tobler *et al.* 2008; Kinnaird & O'Brien 2012; Brodie *et al.* 2015; Yue *et al.* 2015; Wearn *et al.* 2016). Species richness estimation involves attempting to correct for **"imperfect detection"**, i.e. the fact that some species in a given sample may have been missed (**Box 6-1**). Observed species richness will not, in general, be a reliable index of actual species richness because, even if sampling effort is strictly controlled, the **detectability of species will vary** across samples (in most cases, due to variation in abundance). The two principal ways of estimating species richness from camera trap data are with: 1) **non-parametric estimators** (Gotelli & Chao 2013), which use information about the rarest species in the sample to provide a minimum estimate of the number of true species (e.g. Tobler *et al.* 2008), or 2) **occupancy models** (MacKenzie *et al.* 2006). The occupancy-based approaches involve either treating the data from different species as if they were different sampling sites (e.g. Kinnaird & O'Brien 2012), or explicitly modelling the occupancy of each species in the community (including unseen species) and obtaining an estimate of true species richness by summing the occupancies (Iknayan *et al.* 2014; Tobler *et al.* 2015).

It's important to note that the scale over which species richness is calculated can affect the conclusions drawn, and may make it difficult to compare estimates from different studies. Some camera trap studies calculate species richness at the level of an individual camera location – often called **α-richness** (alpha richness) – whilst other studies calculate species richness across a whole study area – often called **γ-richness** (gamma richness). The scale used is important because of the **species-area relationship**: species richness accumulates as the area covered increases, but the rate of this increase may vary in different study sites, meaning that conclusions about which study site is the most diverse may change with scale. Demonstrating this, Wearn *et al.* (2016) found that the effect of logging on mammal species richness was apparently negative at the scale of an individual camera location, but had no discernible effect at the scale of a whole study site.

Whilst species richness is simple to interpret and communicate, it can be a poor measure of biodiversity. In particular, it **weights all species equally**, irrespective of how common they are in the community. For example, a community with a highly skewed relative abundance distribution (with many very rare species) may have the same species richness as a community in which the abundances are much more evenly spread across species. For some purposes, we would prefer a biodiversity measure which down-weights species which are very rare (which might only be represented by one, or very few, individuals in a sample) and focuses on how diverse the more common species are. It is, after all, the more common species which are mostly responsible for the functioning of an ecosystem. **Species diversity indices**, of which there are various types (see Gotelli & Chao 2013), attempt to better capture this notion of biodiversity.

The other major problem with measures of species richness, and indeed species diversity indices, is that they are **insensitive to changes in community composition** (which species are in a community) and **community structure** (the abundance of individual species in a community). This is important because not all species are equal: some are more highly-threatened with extinction than others, and some play highly important roles in their ecosystem (for example being keystone or "engineer" species in extreme cases). One solution is to use a species diversity measure that reflects the types of species present in a community, such as **trait diversity**, **functional diversity**, or even **phylogenetic diversity**. There are very few examples of this being done with camera trap data so far (but see: Ahumada *et al.* 2011). Another solution is to use a measure of community change instead of species richness or diversity (see next, **Chapter 6-2**).

Species richness is often a target for **long-term biodiversity monitoring**, for example with richness estimates compared across years for a given site. For example, O'Brien *et al.* (2011) estimated large mammal richness in Bukit Barisan Selatan National Park, Indonesia over 5 different time points using occupancy models. An occupancy modelling approach also makes it possible to estimate **species colonisation and extinction rates** as a function of covariates (such as body size), whilst accounting for imperfect detection of species (MacKenzie *et al.* 2003, 2006; O'Brien *et al.* 2011). Long-term and standardised camera trap datasets suitable for this kind of analysis are still relatively rare, but the TEAM network sites (many of which have been continuously monitored for > 5 years) are a major exception to this (Ahumada *et al.* 2013; Beaudrot *et al.* 2016).

Further reading: Gotelli & Colwell (2001) provide an accessible introduction to species richness measurement; Gotelli & Chao (2013) give detailed information on estimating species richness and diversity using non-parametric approaches; O'Brien (2008) gives an overview of non-parametric and simple occupancy approaches to species richness estimation for camera traps; Iknayan *et al.* (2014) outline emerging approaches to estimating species richness and diversity, such as multi-species occupancy modelling.

BOX 6-1: DETECTION PROBABILITY, CAPTURE PROBABILITY AND IMPERFECT DETECTION

Detection probability is the probability of a species being recorded, **given that it is present** at a site or sites. In the context of occupancy modelling, detection probability is the probability of recording the species in a single sampling occasion (e.g. a single camera trap night, or however it is defined in the study). Detection probability can be modelled with covariates, so that separate estimates can be obtained for different models of camera trap, different habitats, or different time periods. Sometimes, studies report an **unconditional detection probability,** which is simply the probability of a species being recorded, whether or not it was present in the sampling sites (e.g. it was recorded in 10 of 100 sites, giving an unconditional detection probability of 0.1).

Sometimes, you will see the term detection probability used in reference to capture-recapture and mark-resight modelling, but most researchers use **capture probability** in this context. Capture probability is the probability of an individual animal being recorded in a single sampling occasion. As for detection probability, capture probabilities can be modelled with covariates (e.g. yielding a separate capture probabilities for males and females).

Why do we need to model detection and capture probabilities? This is because sampling in the field is a hit-and-miss affair. Perhaps a species or individual was present in a site, but we didn't leave our camera traps out long enough, we put them in the wrong location, or sometimes the infrared sensors failed to trigger for some reason when animals walked by. We call this the problem of **imperfect detection**. By formally estimating detection and capture probabilities, we can statistically correct for the "misses" and obtain **robust measures** of state variables such as occupancy or density.

6-2 Community variance or β-diversity

When considering two (or more) communities, it is possible to calculate a state variable which reflects the differences between the communities or, more formally, **the variance among the communities.** We sometimes call this community variance "β-diversity" (beta-diversity). This is useful, for example, for assessing the degree to which communities subject to different management differ (e.g. comparing an old-growth site, a selectively-logged site and a plantation forest site). This is sometimes called **"across-site" β-diversity**, because it is being used to assess community variance across heterogeneous habitat types.

β-diversity measures can also be used to assess community variance within single habitat types, at a smaller scale. This is sometimes called **"within-site" β-diversity** (although the distinction from across-site β-diversity may not always be clear-cut). This can be important because changes in community variance within a study site may reflect changes in the fundamental processes which generate biodiversity at local scales (such as habitat heterogeneity and the connectivity of populations).

β-diversity should also play an important role in **spatial conservation planning**, for example in designing networks of reserves. All else being equal, if β-diversity is high, it will be important to establish a network of reserves so that all species in the landscape are covered. On the other hand, if β-diversity is low and communities are similar across space, then a single large reserve may be the best option.

Communities can also be compared across time, rather than across space, giving rise to **temporal β-diversity.** This can be used to track how much, and how quickly, communities are changing at a single site over time.

Camera trap studies typically sample a large number of locations, making them highly suitable for quantifying β-diversity, but this has rarely been done (but see: Wearn *et al.* 2016). At least in part, this is probably because the importance of β-diversity is poorly appreciated amongst wildlife biologists and conservationists. In addition, there are **many different ways β-diversity can be calculated**, each with their own strengths and weaknesses, with no single best measure. This can be confusing and lead to "analysis paralysis". In common with species richness, β-diversity is also dependent on spatial scale (Olivier & Aarde 2014). For example, some habitats such as logged forests may show high β-diversity (rapid community turnover) at fine spatial scales, but low β-diversity (homogenous communities) at coarse spatial scales (Wearn *et al.* 2016). Finally, interpreting and communicating measures of β-diversity can be hard, because they are often in meaningless units, or because they do not lend themselves directly to comparisons across different studies.

6-3 Population abundance

Population counts are central to much of ecology and conservation. The number of individuals of different species determines the much-studied species-abundance distribution, the trophic structure of an ecosystem, the frequency of interactions among species, and the overall functioning of an ecosystem. Population counts are essential for **assessing population** trends of a species, and its response to management or threats to its survival. Local population counts may also feed into global population counts, used in assessing the conservation status of species under IUCN Red List criteria (e.g. see Rademaker *et al.* 2016).

Abundance is a deceptively difficult state variable to measure. This applies to camera traps just as it does to other methods. A huge benefit of camera traps is that they are continuously running, and it is possible to count every individual animal that walks past a camera, unlike say a single-catch live trap which effectively stops recording once it has caught one animal. However, it is usually **difficult to tell individual animals apart in camera trap images**, so that over the course of a week's sampling you often don't know if you have 10 captures of one individual or one capture for each of 10 different individuals. As for species richness, abundance measures are also affected by imperfect detection, so that even if you could tell individuals apart, you will **likely have missed some individuals** in the population. This is the case especially using camera traps, which typically each "see" only a tiny 100 m^2 portion of the ground, and even less in dense vegetation or if the ground surface is not flat. Even if you were to add up the area covered by all of your cameras, and all of the time that they have spent "watching" for individuals, you are unlikely to have achieved a full census of the population.

There are two broad approaches to these fundamental problems: 1) control the sampling methods as much as possible and use an index of true abundance **(Chapter 6-3-1**), or 2) explicitly try to model the process by which animals are detected and obtain an estimate of absolute abundance (**Chapter 6-3-2**). We focus here (in **Chapter 6-3**) on abundance (the number of individuals in a population), and then (in **Chapter 6-4**) deal with density (the number of individuals per unit area).

6-3-1 Relative abundance indices

The simplest way of analysing the data is to use the frequency of animal detections, or trapping rate (typically, detections per 100 nights of camera trap sampling), as an **indirect measure of abundance** (see **Box 6-2** for how detections are counted in practice). This is often referred to as relative abundance – to distinguish it from actual absolute abundance – and the resulting measure is often called a relative abundance index (RAI). Clearly, trapping rates are going to be influenced by much more than just the abundance of animals. For this reason, they have been **highly controversial** (e.g. Anderson 2001; Sollmann *et al.* 2013c). For example, trapping rates will be affected by how active animals are (animals which are active for longer or cover more ground will trigger the cameras more) and how large they are (animals which are larger are more likely to be detected by the passive infrared sensors on most camera traps). However, attempts can be made to standardise at least some of the factors that affect trapping rates **by very carefully designing** the study (see **Chapter 7-6**). It is also possible to estimate the **size of the detection zone** of the camera traps in different habitats or for different species and apply corrections to the indices (Rowcliffe *et al.* 2011).

A simple way of estimating the effective detection distance (i.e. the detection zone's radius) is to place markers in the field of view at known distances, and then record the approximate distance at which animals are detected (Caravaggi *et al.* 2016; Hofmeester *et al.* 2017; **Fig. 6-1**). The effective detection distance can then be estimated using distance sampling methods (Hofmeester *et al.* 2017). A short cut to controlling for variation in detection distances is to only count animal detections within a short distance that is unobstructed and well sampled across all cameras and all species (e.g. 3 m, indicated by a marker placed in the field of view). However, this will necessarily involve discarding a portion of the dataset.

Despite the controversy that RAIs invoke, their judicial use **can still offer meaningful insights** into wildlife populations. In addition, where RAIs have been **compared to robust density estimates**, the correlations across space (Rovero & Marshall 2009), across studies (Carbone *et al.* 2001), and even across species (O'Brien *et al.* 2003; Rowcliffe *et al.* 2008; Kinnaird & O'Brien 2012) have usually been positive and apparently linear.

Figure 6-1. Camera trap image of a European pine marten (*Martes martes*) in a Dutch woodland with dense underbrush. Two distance markers (at 2.5 and 5 m) have been placed in the field of view (highlighted with red boxes), which can be used to correct for variation in the effective detection distance (i.e. the radius of the camera trap detection zone). Image © Tim Hofmeester.

Further reading: Sollmann *et al.* (2013c) give a firm critique of relative abundance indices in camera trap studies. For an alternative view, see Johnson (2008), who encourages criticism of indices but argues that they can still be useful. Banks-Leite *et al.* (2014) also argue that, with careful study design, indices (and other "unadjusted estimates") can be a useful and cost-effective option.

6-3-2 Capture-recapture, mark-resight and the Royle-Nichols model

The second broad approach to estimating abundance from camera trap data is to attempt to describe, using a model, the ecological and methodological processes which gave rise to the data. By doing this, it is possible to obtain an estimate of absolute abundance, i.e. the number of individuals in a population. This could be the number of individuals in a fenced reserve or on an island. Note that in a continuous habitat, what a "population" is can be difficult to define, and density is often a more useful target for monitoring (**Chapter 6-4**).

A well-known approach to obtaining an estimate of absolute abundance is capture-recapture (Otis *et al.* 1978; White *et al.* 1982; Foster & Harmsen 2012; **Fig. 6-2**). Capture-recapture methods, as applied to camera-trapping, exploit the fact that a species may be **individually-identifiable** in camera trap images or videos (either through natural markings, or markings applied by researchers, such as radio collars). By using information on how readily animals are recaptured once they have already been seen once, capture-recapture models can estimate how many **unseen animals** remain in the population (Otis *et al.* 1978). Although this method is widely used in ecology, only a narrow subset of species appearing in camera traps naturally have unique markings (typically < 5% of species).

A closely-related method to capture-recapture is the mark-resight approach for **"partially-marked" species** (Arnason *et al.* 1991; McClintock *et al.* 2009). In some species, only a subset of individuals might have distinctive characteristics and can be reliably identified, and the rest of the population are unmarked. The marks on animals may be naturally-occurring characteristics (e.g. scars or antler shapes), or they can be marks that have been added by researchers (e.g. radio collars or ear tags).
Just as in capture-recapture, mark-resight models arrive at an estimate of abundance by controlling for capture probabilities, but they also incorporate information from the **number of sightings of unmarked individuals.** This complication is reflected in how the data is recorded under the mark-resight approach; captured animals now fall into

BOX 6-2: HOW DO I COUNT THE NUMBER OF DETECTIONS MADE BY A CAMERA TRAP?

A unique aspect of calculating relative abundance indices is that two different people may count the number of detections made by a camera trap differently. This is not the case for occupancy and capture-recapture analyses, which just involve recording a detection or non-detection (usually denoted by a "1" and a "0", respectively) in a specified window of time.

Perhaps the most objective way of counting the detections made at a sampling point is to **count every time an animal enters the camera trap's detection zone.** For practical purposes, the detection zone can be assumed to be the field-of-view of the images. If an animal leaves the detection zone (or field-of-view) momentarily and comes back in, then that is counted as a new detection. Indeed, this is how detections should be counted for the random encounter model (Rowcliffe *et al.* 2008; Chapter 7-8).

However, in most cases, this is not how detections are counted for RAIs. Instead, decisions are often made about whether detections are **"independent"**. The definition of independence varies from study-to-study, but the typical definition is a detection that is separated by a **sufficient amount of time** from the previous detection, or that clearly involves a **different individual** (e.g. O'Brien *et al.* 2003). The time interval between independent detections that is used varies across studies, but an arbitrary 30 minutes (e.g. O'Brien *et al.* 2003; Gerber *et al.* 2010; Kitamura *et al.* 2010; Samejima *et al.* 2012) or 1 hour (e.g. Tobler *et al.* 2008; Rovero & Marshall 2009) are the most common. Note that the time interval will make little difference to the RAI for a species which typically appears in front of camera traps for only a fleeting moment (e.g. a top carnivore, with fast and directed movements), but will have a much larger effect on the RAI for a species which moves slowly and circuitously (e.g. a herbivore, such as a deer).

one of three categories: 1) they are identifiable (in which case, the identity is recorded), 2) they are known to be marked but cannot be identified on that instance (e.g. because only part of the animals is visible in the image), or 3) they are simply unmarked. Mark-resight models were among the first robust models ever applied to camera trap data (e.g. Mace *et al.* 1994), but have since only been **rarely used** (e.g. American black bears: Martorello *et al.* 2001; fisher: Jordan *et al.* 2011; Florida Key deer: Watts *et al.* (2008); puma: Rich *et al.* 2014). Newer, spatial versions of these models (**Chapter 6-4-3**) may make the mark-resight approach become more widely used with camera traps in future.

Capture-recapture and mark-resight models can also offer a window into **population vital rates**, such as survival probabilities and recruitment rates. For this, it is necessary to carry out monitoring over multiple years using the so-called **"robust design"** (e.g. Karanth *et al.* 2006). Essentially, this is just repetition of a standard closed population capture-recapture or mark-resight study multiple times (e.g. over multiple seasons or years). Mondal *et al.* (2012) used the robust-design to estimate leopard abundance, survival and recruitment over 5 years of sampling in Sariska Tiger Reserve, India. Using the leopard abundance estimates for each year, they also calculated the mean annual population growth rate, a useful state variable for management. Jordan *et al.* (2011) used a robust design implementation of a mark-resight model to estimate fisher (*Martes pennanti*) abundance and annual survival probabilities over 3 years of sampling in the Sierra Nevada mountains of California, USA. Note that survival and recruitment under the robust design are technically **"apparent" survival and recruitment** rather than true estimates, because the models assume that individuals which appear or disappear must have recruited or died, respectively, when they could have instead just immigrated or emigrated permanently.

An alternative to models which require all or some of a population to be marked is the "Royle-Nichols" model (Royle & Nichols 2003; MacKenzie *et al.* 2006). This model was originally devised for bird point count data (Royle & Nichols 2003), and was devised as a way to relax the assumption of constant abundance in occupancy models (see **Chapter 6-5**). However, since then, it has also been applied to camera trap data (Brodie *et al.* 2014; Granados *et al.* 2016; Linden *et al.* 2017; Wearn *et al.* 2017). The basic idea is that, if individual detection probability is assumed to remain constant, variation in species-level detection probability across sites therefore betrays information on the local abundance of animals at those sites. Crucially, the model **does not require that individuals are distinguishable,** which is ideal for camera trap data, and simply uses the sequence of detections and non-detections recorded at each of the camera trap locations. The drawback to the method is that it **assumes a relatively specific relationship** between local abundance and species-level detection probability, which may not hold in practice.

Capture-recapture, mark-resight and Royle-Nichols models simply output an estimate of the absolute number of individuals. For capture-recapture and mark-resight this is the number of individuals exposed to sampling by a trapping grid, whilst for Royle-Nichols models it is the number of individuals exposed to sampling by a single camera trap location. Just as for species richness, **absolute abundance is related to the size of the area that is sampled,** which is not specified in these analyses. Absolute abundance may sometimes be of interest in closed systems (such as isolated patches of habitat) or if populations are very small (and therefore potentially subject to small population size effects, such as inbreeding depression), but most commonly we would like to control for sampling area to allow for better comparisons across studies. This is more difficult than it sounds, since animals are often moving in and out of your notional sampling area, but methods do exist (see next, **Chapter 6-4**).

Further reading: See White *et al.* (1982) and McClintock & White (2012) for introductions to capture-recapture and mark-resight methods, respectively; see MacKenzie *et al.* (2006) for information on the Royle-Nichols model and its application.

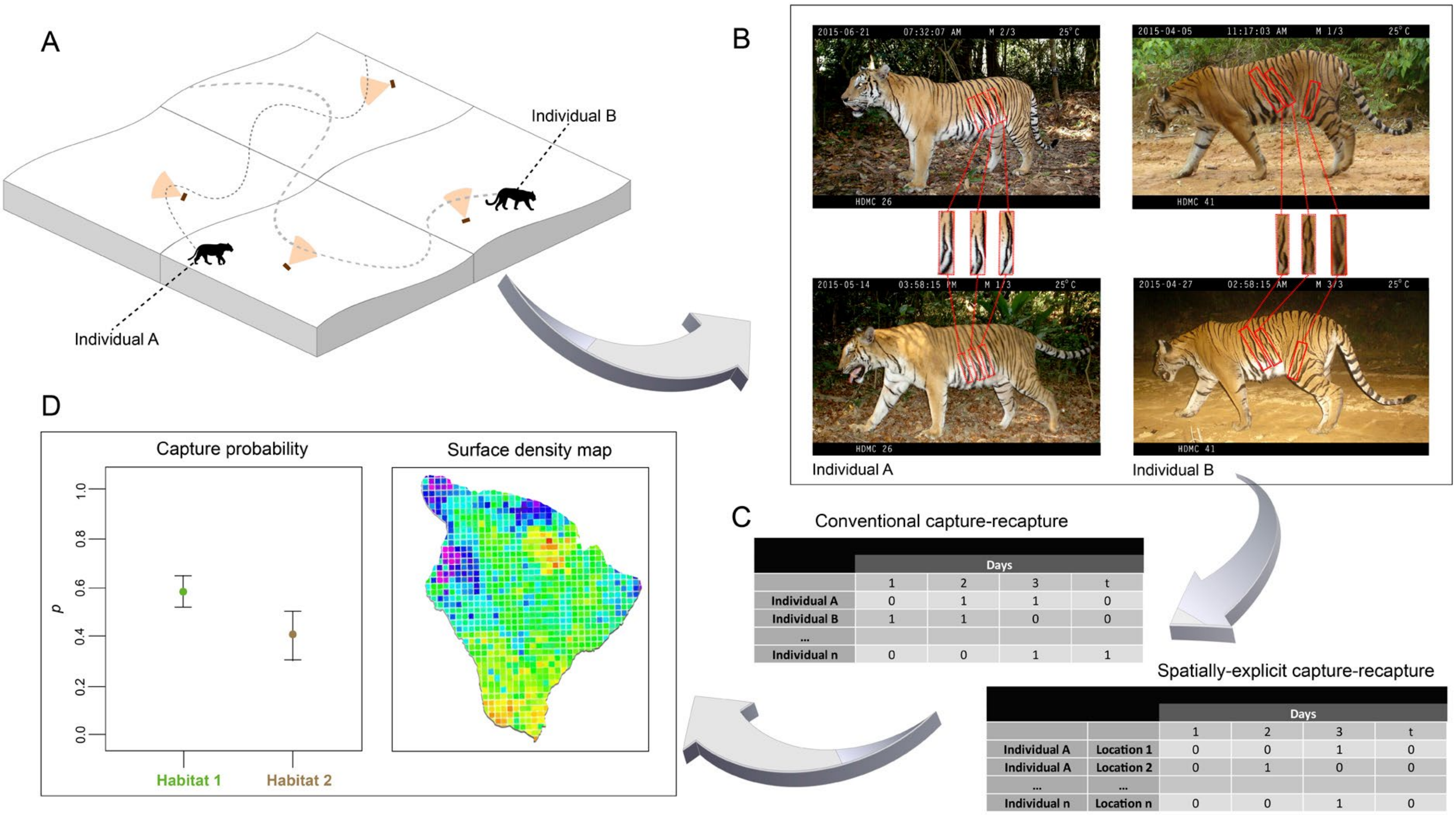


Figure 6-2. The capture-recapture approach to camera-trapping. Camera traps are set up to capture multiple individual animals, ideally with captures of each occurring across multiple locations (**A**). Individual animals are matched across images at different times and locations (**B**). Capture histories are built for each individual (**C**). Modelling can be used to control for capture probabilities and (for spatially-explicit methods) map density across space, for example in a protected area (**D**). Just two individuals and four sampling locations are shown here for demonstration; studies should ideally sample > 40 locations and capture > 10 individuals (**Chapter 7-7**). Camera trap images © Mark Rayan Darmaraj/Christopher Wong/ WWF-Malaysia.

6-4 Population density

The number of animals per unit area (e.g. per km^2), or population density, is often considered the **"gold-standard" state variable** in wildlife studies. Unlike measures of abundance, and especially relative abundance, it allows for much more **direct comparisons** across studies (even if they use vastly different methods) and across species. However, it is perhaps **the hardest state variable to measure** and can often therefore be very **costly to achieve**.

Much of the difficulty lies in the fact that, even if an estimate of abundance can be made (e.g. using the approaches in **Chapter 6-3-2**), the **effective sampling area** that this corresponds to is not easily calculated. The effective sampling area may be smaller than the area covered by the camera-trapping grid, for example if it contains areas which are not suitable habitat for a species (such as water bodies, for a terrestrial species). More often, though, the effective sampling area will be larger than the area notionally covered by sampling, because the animals captured also spend time outside the sampling grid.

6-4-1 Ad-hoc calculation of effective sampling area

One approach to obtaining population density, which was used in the iconic early papers by Ullas Karanth and Jim Nichols (Karanth 1995; Karanth & Nichols 1998), is to make an estimate of abundance using capture-recapture methods, and then divide this by an ad-hoc estimate of the effective sampling area. Here, effective sampling area is typically calculated by adding a **"boundary strip" of half the diameter of an average home-range** onto the outside of the trapping grid. Ideally, home-range estimates should be derived from high-resolution movement data (e.g. from a GPS- or radio-collar), but most often they have been estimated from the **maximum displacement distances** observed inside camera-trapping grids. This home-range measure obtained from the trapping grid is often called "half the mean maximum distance moved" (½MMDM). Where data is sparse, or where camera-trapping grids are small relative to the movements of a species, the use of ½MMDM will usually lead to an underestimation of home-ranges and therefore an **overestimation of density.** This has often led to arbitrary adjustments being applied, such as using one whole home-range diameter, i.e. MMDM instead of ½MMDM. There is no theoretical justification for this approach (Parmenter *et al.* 2003), but it seems to lead to low bias in simulations (Tobler & Powell 2013). It also leads to estimates that are much closer to those based on spatially-explicit methods (see next, **Chapter 6-4-2**) than when using ½MMDM (Soisalo & Cavalcanti 2006; Sharma *et al.* 2010; O'Brien & Kinnaird 2011; Gerber *et al.* 2012).

6-4-2 Spatially-explicit capture-recapture (SECR)

Although the ad-hoc method of calculating density was widely adopted in camera-trapping studies (in particular of felid species), and had substantial precedent in studies of small mammals, it was long known to be problematic (Foster & Harmsen 2012). Efford (2004) developed a model which explicitly considered the spatial dimension of the data, incorporating information on the exact **locations of traps** (their geographic coordinates) and **where captures of individual animals were made**. This model was later developed further and applied to camera trap data (Royle *et al.* 2009a, b). These methods are referred to as "spatially-explicit capture-recapture" (SECR). In essence, these models exploit information about home-range sizes by looking at how far apart the captures of each individual are, much like the ad-hoc methods outlined above do, but they incorporate the estimation of density and effective sampling area into **one single, elegant model**. In particular, the effective sampling area is no longer a hard imaginary boundary strip drawn around a trapping grid, but a diffuse "halo" of declining capture probability as one goes further away from each camera trap.

SECR has now been used in dozens of camera-trapping studies, primarily of spotted and striped felid species:

- African golden cat (Bahaa-el-din *et al.* 2016)
- Andean cat (Reppucci *et al.* 2011)
- Eurasian lynx (Blanc *et al.* 2013)
- Jaguar (Sollmann *et al.* 2011)
- Leopard (Gray & Prum 2012)
- Leopard cat (Srivathsa *et al.* 2015)
- Marbled cat (Hearn *et al.* 2016)
- Ocelot (Rodgers *et al.* 2014)
- Pampas cat (Gardner *et al.* 2010)
- Snow leopard (Alexander *et al.* 2015)
- Sunda clouded leopard (Wilting *et al.* 2012)
- Tiger (Sunarto *et al.* 2013)
- Wildcat (Anile *et al.* 2014)

The method has also been used on a limited number of other species that are individually identifiable, including:

- Asian bear species, sun bear and Asiatic black bear (Ngoprasert *et al.* 2012)
- Hyena species (O'Brien & Kinnaird 2011; Singh *et al.* 2014)
- Malagasy civet (Gerber *et al.* 2012)
- Orangutan (Spehar *et al.* 2015)
- Puma (Quiroga *et al.* 2016)
- Tapir species (Rayan *et al.* 2012; Tobler *et al.* 2014)
- Wolverine (Royle *et al.* 2011)

Capture-recapture methods have, until recently, meant binning capture data into sampling occasions, meaning that multiple captures within a sampling occasion are ignored. New developments in SECR modelling have allowed for the **incorporation of capture times**, as well as locations, which means that none of the spatial and temporal data recorded by camera traps is discarded (Borchers *et al.* 2014; Dorazio & Karanth 2017). This can potentially lead to less biased and more precise estimates of density (Borchers *et al.* 2014), as well as revealing animal distribution patterns (Dorazio & Karanth 2017). In practice, the benefits of using these continuous-time models are likely to be most important for large datasets involving hundreds of captures.

There is also an **open population variant of SECR**, which allows density to vary across years and provides an estimate of population vital rates as well (Gardner *et al.* 2010). As for open models for conventional capture-recapture, this uses the robust design, requiring multiple years of sampling. This model has been relatively poorly explored to date, but was used to estimate density, survival and recruitment for a population of Pampas cats (*Leopardus pajeros*) in Argentina over just a short 2 year period (Gardner *et al.* 2010).

SECR has now **largely supplanted the ad-hoc adjustment method** based on non-spatial capture-recapture. Fundamentally, however, SECR still depends on being able to individually identify animals in camera trap images. Two further methods of density estimation exist for the more common cases where only some individuals of a species are identifiable (**Chapter 6-4-3**), or where they are never identifiable (**Chapter 6-4-4**).

6-4-3 Spatially-explicit mark-resight

There is also an equivalent modelling approach to SECR, but for **partially-marked populations**. Spatially-explicit mark-resight (sometimes written just as "spatial mark-resight") is a new approach which offers to incorporate the spatial recapture information from marked individuals, alongside the captures of all other unmarked individuals, and **directly produce a density estimate** (Chandler & Royle 2013). Much like the SECR methods for completely-marked populations, this approach crucially depends on the information revealed by recaptures of individuals in multiple camera traps. The approach has only been applied to camera trap data from two species so far – puma, *Puma concolor* (Sollmann *et al.* 2013a; Rich *et al.* 2014) and racoon, *Procyon lotor* (Sollmann *et al.* 2013b) – but the approach offers great potential for a wider range of species. In principle, this method also allows for density estimation for a **completely unmarked population**, but the precision of the density estimates in such cases is likely to be so low as to be of **limited practical value** (Borchers & Fewster 2016).

Chandler & Royle's (2013) spatially-explicit model has been extended to deal with detection/non-detection data, rather than detection counts, which may be more suited to camera trap data (Ramsey et al. 2015). However, the same problem of low precision in the density estimate remains a feature of this model when it is used on completely unmarked populations (Ramsey et al. 2015)

6-4-4 Random encounter modelling (REM)

When individuals of a species are completely **unmarked** (i.e. unidentifiable), the only practical option for estimating density is to use random encounter modelling (REM; Rowcliffe *et al.* 2008). REM has few mathematical details in common with other modelling approaches to camera trap data, and comes from a completely separate origin. In fact, it comes from an ideal gas model, modified to better approximate the process by which animals and camera traps come into contact (in particular the fact that animals only make "contact" with a camera inside a wedge-shaped detection zone projected in front of the camera, rather than from any angle). The parameters in the REM equation are:

- **Trapping rate** (**Chapter 6-3-1** and **Box 6-2**)
- Animal **speed**
- Animal **activity level** (the proportion of time animals spend active and available for detection by cameras)
- Dimensions of the camera **detection zone** (approximated by a 2D cone shape, with angle and radius parameters)

Validation of the estimates produced by this method have shown that it is able to recover known animal densities in captive environments (Rowcliffe *et al.* 2008), and **correlates well with estimates from other methods** (e.g. African lion: Cusack *et al.* 2015b; Grevy's zebra: Zero *et al.* 2013; hare species: Caravaggi *et al.* 2016; paca: Suselbeek 2009; wildcat: Anile *et al.* 2014).

Although REM is a promising method for obtaining density estimates for a wide range of species, it makes a set of unique demands of the camera-trapper. Whilst the model does not assume that animals move strictly randomly (which they emphatically do not), it does assume cameras are deployed randomly with respect to their movements (Rowcliffe *et al.* 2013). In practice this means that **simple random or systematic random sampling designs** should be used (this can be combined with stratification as necessary; **Chapter 7-3**). In addition, some of the parameters of the REM equation are **difficult to estimate**, and may remain completely unknown for the vast majority of species. Animal speed has traditionally been derived from radio-tracking studies, which are costly and logistically difficult. Ideally, the estimate of animal speed should also be made concurrent with the camera-trapping, in the same study area (Rowcliffe *et al.* 2016).

These special requirements of REM have slowed its uptake as a general method for monitoring wildlife. However, the main obstacles to its implementation are in the process of being overcome by **developments in technology**. Firstly, randomised placement is increasingly becoming an acceptable strategy for camera-trapping due to developments in camera technology (e.g. Wearn *et al.* 2013; Cusack *et al.* 2015a). Camera traps have greatly improved in their efficiency as data-generating devices; **no longer is it absolutely necessary to target only trails and use attractants** in order to obtain sufficient sample sizes for a wide range of analyses. Secondly, it has recently been demonstrated that it is possible to turn camera traps into wildlife "speed cameras", in order to obtain an estimate of animal speed (Rowcliffe *et al.* 2016). The "brute-force" approach to this is to review any captured camera trap videos (or "near-video" sequences of images) in the field and then make measurements of animal movements manually, using a tape measure (Rowcliffe *et al.* 2016). These measurements can also provide estimates of the detection zone parameters for each species (Rowcliffe *et al.* 2011). A more sophisticated method involves **"calibrating" camera traps** during setup or pickup, by triggering cameras to take images of an **object of known** size at various distances (**Fig. 6-3**). Theoretically, this allows for the reconstruction of animal movement paths along a ground surface using just the pixel positions of animals within camera trap videos and information about the camera lens (Rowcliffe *et al.* 2016). Since the time taken to complete each movement path is also recorded by the camera trap (as shown in the date-time stamp on the videos or images), it is possible to calculate animal speed. In this case, no measurements have to be made in the field at all, saving considerable time and labour.

Figure 6-3. Turning a camera trap into a wildlife "speed camera" using camera calibration techniques. Images or videos are taken of an object of known size (here, a 1 m pole) placed at different locations (e.g. 20) within the camera trap's detection zone (**A**). Given information about the camera trap's lens, it is possible to calculate the distance and angle of the object from the camera in each of the locations, as well as model the values for intervening locations. The model relates pixel locations in the image to distances and angles in the real world. Animals are then tracked in image sequences or videos (**B**) and the distances and angles calculated from the model. These values are used to estimate the detection zone parameters of the camera trap (radius and angle) and reconstruct animal movements.

Further reading: See Rowcliffe *et al.* (2008), Rowcliffe *et al.* (2011), Rowcliffe *et al.* (2014), and Rowcliffe *et al.* (2016) for detailed explanations of each of the steps in the REM method.

		Abundance state variable of interest		
		Relative abundance	Absolute abundance	Population density
Type of population	"Unmarked"	Trapping rate (Chapter 6-3-1)	Royle-Nichols (Chapter 6-3-2)	Random encounter modelling (Chapter 6-4-4)
	"Partially-marked"	-	Mark-resight (Chapter 6-3-2)	Spatially-explicit mark-resight (Chapter 6-4-3)
	"Marked"	-	Capture-recapture (Chapter 6-3-2)	Spatially-explicit capture-recapture (Chapter 6-4-2)

Table 6-1. Summary of the abundance estimation methods that are suitable for camera trap data, depending on the state variable of interest and the type of population under consideration. Individuals in "unmarked" populations are not obviously identifiable, whilst "partially-marked" and "marked" populations consist of individuals some or all of which can be identified.

6-5 Species occupancy

Species occupancy – whether a species occurs in a site or not – has long played a role in ecology and conservation biology. In particular, occupancy patterns have been used to address biogeographical questions (Diamond 1975) and in the study of metapopulation dynamics (Hanski & Hanski 1998). In addition, occupancy is also highly suitable for studying broad-scale species distribution patterns. However, the more recent rise in popularity of occupancy arguably has more to do with practicalities: occupancy offers a way of robustly monitoring many populations for which it is not possible to robustly monitor abundance. Occupancy only **requires detection/non-detection data** for modelling and is therefore often **cheaper** and **more easily studied** than abundance, and can be applied to a **wide range of species**. For these reasons, the Wildlife Picture Index standardised protocol (O'Brien *et al.* 2010) and the TEAM global network (Beaudrot *et al.* 2016) both use occupancy as their state variables of choice.

Occupancy is clearly related to abundance (being the probability that a site has ≥ 1 individuals), and some studies have shown a good correspondence between the two (Clare *et al.* 2015; Linden *et al.* 2017). However, they remain fundamentally different state variables, with occupancy only functioning as an **index of abundance under strict conditions** (Efford & Dawson 2012). Occupancy may be highly insensitive to changes in abundance (it makes no distinction between sites with 100 animals versus sites with just one animal), especially if occupancy is measured coarsely with respect to the home-range of an individual animal. It is also possible for changes in occupancy to occur without changes in abundance, for example if home-range sizes of animals, or their extent of overlap, vary over space or time (Efford & Dawson 2012).

Occupancy estimates can be interpreted in a number of different ways, which can be problematic when making inferences about populations and when communicating results. Occupancy is defined formally as the **probability that a site is occupied**, but the specific interpretation of this depends in turn on how a site is defined. A site may be naturally defined, for example an island or habitat fragment, or it may be artificially defined, typically as a grid cell (e.g. 1 km^2 of habitat). In some circumstances, it is possible to interpret occupancy also as the proportion of sites that are occupied or, more specifically, the **proportion of area that is occupied** (PAO) in a study region. These interpretations come with the additional assumption that sampled sites are indeed representative of unsampled sites and the broader study region. Note that PAO is only technically estimable from sampling methods which are point-based, such as camera traps (Efford & Dawson 2012).

The size of a site relative to the size of an animal's home range also has implications for the interpretation of occupancy. If animals range over a much larger area than a single site, then a) they may conceivably be unavailable for capture during a sampling occasion, and b) the "occupancy" of a site is more related to the ranging patterns and habitat preferences of an individual, rather than the coarse-scale distribution of a species. As a result, when reporting occupancy estimates for species with home-ranges larger than a single site, **"probability of use"** is preferred over "probability of occupancy" (Mackenzie & Royle 2005).

Further reading: See MacKenzie *et al.* (2006) for an accessible text on occupancy modelling.

Occupancy can also be studied over time using long-term camera trap datasets. "Open" occupancy models exist which allow for the estimation of site colonisation and extinction probabilities, including the incorporation of covariates to explain variation in these variables (MacKenzie *et al.* 2003, 2006). This information is critical to the understanding of how species are faring in fragmented landscapes, and why certain species are suffering from range collapses.

Finally, occupancy models can offer a way of investigating the strength of interactions among species, whilst correcting for imperfect detection. Models exist for two interacting species (Mackenzie et al. 2004; Rota et al. 2016b), or several interacting species (Rota et al. 2016a). For example, Rayan & Linkie (2016) investigated pairwise co-occurrence patterns among tigers, leopards and dholes in Malaysia using camera-trapping.

State variable	Pros	Cons
Species richness	• Fundamental to much ecological theory and often a key metric used in management • Simple to analyse, interpret and communicate • Models exist to estimate asymptotic species richness, including unseen species (simple versions of these models are implemented in EstimateS and the "vegan" package in R)	• Dependent on scale (as captured in the species-area relationship) • All species have equal weight in its calculation, and community evenness is disregarded • Insensitive to changes in abundance, community structure and community composition
Species diversity	• Attempts to better capture common notions of biodiversity, by capturing evenness as well as richness (although, note that some indices only reflect evenness) • Most indices are easy to calculate and are widely implemented in software packages (e.g. EstimateS and the "vegan" package in R)	• A multitude of diversity indices exist, and it can be difficult to choose the most appropriate • Interpretation and communication of results may not be straightforward (e.g. the Simpson index is "the probability that two species chosen at random from the sample are the same") • Insensitive to changes in community composition
β-diversity	• Can be used to track changes in community composition • Plays a critical role in effective conservation prioritisation (e.g. designing reserve networks or conservation set-aside) • Important for detecting changes in the fundamental processes generating local biodiversity	• There are a vast number of measures to choose from, each with their own properties, and no single measure is best for all purposes • Comparing measures across space, across time and across studies can be very difficult • Dependent on scale (i.e. the size of the communities that are being included)
Relative abundance	• Simple to calculate, and technically possible even with small sample sizes when robust methods might fail • Studies have shown that relative abundance measures often do track robust measures of abundance • Calibration with independent density estimates is possible	• Difficult to make inferences from, due to the large number of assumptions that must hold in order for changes to accurately reflect changes in actual abundance; this makes comparisons across space, across time, across species and across studies very difficult • Requires more stringent survey design, including the use of random sampling points, standardised methods (such as the camera model used) and no baiting

State variable	Pros	Cons
Absolute abundance: capture-recapture and mark-resight	• Abundance is a fundamental parameter in ecological theory, and an accurate estimate is essential for the management of small or discrete populations • May be used as a relative abundance measure that controls for imperfect detection • Easy-to-use, if now rather dated, software exists to implement capture-recapture (CAPTURE); MARK implements more complicated models with covariates (and must be used for mark-resight modelling) • Can use the robust design with "open" models to obtain recruitment and survival rate estimates	• Requires that individuals are distinguishable in camera trap images (most species are unmarked) • Depends on sampling area, which is difficult to calculate (principally because animals detected in the trapping area also spend time further afield), unless animals are tagged and tracked as part of the study • Requires that a minimum number of individuals are captured, and that a sufficient number of recaptures are also made • Relatively stringent requirements for survey design, in particular the requirement for there to be no "holes" in the trapping grid • For mark-resight, animals may have to be physically captured and marked if natural marks do not exist on a sufficient number of individuals
Absolute abundance: Royle-Nichols model	• As for capture-recapture, abundance is a fundamental parameter in wildlife ecology and in monitoring • Can be applied to species which are unmarked • Just requires detection/non-detection data for each site as the input, not counts • As for capture-recapture, may be used a relative abundance measure that controls for imperfect detection	• As for capture-recapture, depends on sampling area • Assumes a specific relationship between abundance and detection probability, which may not hold • No dedicated, simple software for this model (but can be implemented in MARK and the "unmarked" package in R)
Population density: capture-recapture with ad-hoc calculation of effective sampling area	• The easiest way to obtain population density for a species in which individuals are identifiable • It may be useful to use this method to allow for direct comparisons with historical estimates for a given species	• Involves capture-recapture methods, and the drawbacks that come with that (see above) • Requires good data on home-range sizes of the species (e.g. from radio-tracking), ideally from the same study area; this can be done from the camera-trapping data itself, though this requires very large trapping grids and sufficient recaptures • Represents the effective sampling area as a hard boundary (individuals are either trappable or not, rather than their detection probability being a function of how far their home range centre is away from the trapping grid)
Population density: spatially-explicit capture-recapture (SECR)	• Estimates are fully comparable across space, across time, across species and across studies • Density estimates are obtained in a single model, fully incorporating the spatial information that is also obtained during a camera trap survey (i.e. where the camera traps are in space, and where the captures of each individual were made) • Both likelihood-based and Bayesian versions of the model have been implemented in relatively easy-to-use software (DENSITY and SPACECAP, respectively, as well as associated R packages) • Allows for great flexibility in survey design, for example allowing "holes" in the trapping grid • "Open" SECR models exist, allowing for recruitment and survival rate estimation	• Requires that individuals are distinguishable in camera trap images (most species are unmarked) • As for capture-recapture, requires that a minimum number of individuals are trapped (each recaptured a number of times, ideally), but also that individuals are captured in a number of different camera locations

State variable	Pros	Cons
Population density: spatially-explicit mark-resight	• As for SECR of fully-marked species, estimates are fully comparable • Can be applied to a broader range of species than SECR, and allows researchers to mark a subset of the population (as might happen anyway with radio-collaring) or to take advantage of any natural markings (such as injuries or antler shape)	• Remains poorly-tested with camera trap data, although it offers promise (simulations and field validation are needed) • Density estimates are likely to be less precise than with SECR or random encounter modelling, unless a large proportion of the population have marks • As for SECR, requires sampling points to be sufficiently close such that individuals come into contact with multiple cameras
Population density: random encounter modelling (REM)	• As for SECR, estimates are fully comparable • Can be applied to species which are unmarked, allowing for community-wide estimates of density • Also outputs ecologically- and methodologically-informative parameter estimates in the process (including animal speed, activity levels and detection zone parameters of cameras)	• Requires relatively stringent survey design, in particular the use of random sampling points and no baiting; otherwise, survey design is quite flexible (e.g. "holes" in trapping grids are allowed, and camera spacing is less important) • Requires independent estimates of animal speed (e.g. from radio-tracking) or the measurement of animal speed within camera trap videos (either by taking manual measurements in the field, or by "calibrating" cameras in the field) • No dedicated, simple software for this model (this is currently in development), although R scripts are available
Occupancy	• Just requires detection/non-detection data for each site as the input, not counts • Relatively easy-to-use software exists for fitting models (PRESENCE); also implemented in MARK and the "unmarked" R package • "Open" models exist which allow for estimation of site colonisation and extinction rates • Multi-species occupancy models allow for interactions among species to be investigated whilst controlling for imperfect detection	• Although some studies have shown that occupancy measures track robust measures of abundance, occupancy only measures distribution; it may be an insensitive, or even misleading, indicator of abundance changes (e.g. changes in occupancy may occur due to changes in range size) • Interpretation and communication of results may not be straightforward if the scale of movement of a species is much larger than the trap spacing ("probability of use" rather than "probability of occupancy")

Table 6-2. Summary of the positives and negatives associated with the main state variables which can be investigated using camera traps.

Camera traps can be used to estimate various population and community state variables. For example, they can be used to monitor the abundance and distribution of a rare species. However, in order to do this effectively, best-practice must be followed in terms of the sampling design and field protocols.

Image of a banteng, *Bos javanicus*, in Borneo: © Oliver Wearn

7 DESIGNING A CAMERA TRAP STUDY

HIGHLIGHTS

- Well-designed and useful camera trap studies have clear answers to the "what" and "why" questions: what is it you would like to know, and why exactly?
- Having identified your "what" and "why", you can think about "how" you are going to achieve your aims, by identifying constraints on your study, the relevant scale of sampling, and any state variables you will need to estimate
- Camera trap sampling should, in the first instance, be designed with the basic principles applied across the rest of ecology: randomisation, replication and stratification
- If your aim is to test a hypothesis, e.g. that mammal abundance is reduced in hunted areas, then you need to think carefully about confounding variables and pseudo-replication when designing your study
- Having identified any state variables you aim to estimate, make sure you understand the assumptions inherent to the method, as these will guide you in designing your sampling
- Species check-listing involves no formal modelling or assumptions, and there is therefore complete flexibility on sampling design
- Species richness and diversity estimation involves assumptions of random and independent sampling, so sampling designs should obey standard principles of sampling, including random placement of cameras (unless occupancy-based methods will be used)
- The use of relative abundance indices involves strong assumptions about constant detection probabilities (e.g. over space, time or species) which will rarely be met; great efforts should be made to standardise as much of the sampling as possible (e.g. by using only a single model of camera trap and placing cameras randomly)
- Capture-recapture methods come with a number of well-defined assumptions and, as long as these are met, there is a large amount of flexibility on sampling design (especially with spatially-explicit capture recapture methods)
- Random encounter modelling makes strong assumptions about how camera traps and animals interact, and random camera placement is essential
- Occupancy can be estimated from either grid- or point-based designs; the latter makes stronger assumptions about camera placement, but offers stronger inferences about occupancy (in particular, allowing the proportion of area covered by the species to be estimated)
- Appropriate sampling designs for monitoring animal behaviour and the activities of people (e.g. illegal poaching) are highly-dependent on the aims of a study, as well as any assumptions that will be made during statistical modelling of the data

7-1 Study aims: establishing the "what" and the "why"

The starting point for planning your use of camera traps is to establish **"what" it is you would like to know**. For example, you might want to know where a species is found, or how it responds to certain threats. Your study's aims do not have to be cutting-edge or complicated, but they do have to be explicit. If you can state your aims in the form of a question, all the better. The clearer you are about your aims at the earliest possible stage, the smoother the planning and execution of your study will be.

As well as determining "what" your study is about, you should also ask **"why" you are doing it**. You will likely know the context of your study very well, but it can be useful to pause and reflect broadly on your study system as you formulate your aims. Consider what management options are available for your species or landscape and, in turn, how the aims of your study fit into that broader context. For example, what hypotheses do you need to test to aid decision-making, or what information will you need in order to actually implement any proposed management actions?

As well as explicitly stating your aims, you should also **define your constraints** at this stage. These may be constraints to do with resources, capacity, logistics and the interests of any stakeholders. These constraints will set the practical limits on what is actually achievable, which may feed back into your aims and cause you to re-evaluate them.

This is also the stage at which you should attempt to **become an expert** in the topic and species of interest. Research previous work that has been done and consult extensively with relevant experts, both on the topic and on the local context. On the basis of all this, identify what aspects of your study system you can actually form evidence-based conclusions about, and what aspects of it contain genuine gaps in available knowledge. Stand on the shoulders of giants.

You should also think about the **scale of your study**: is it at the scale of a species geographic range, at the national scale, or at the local scale of a single study site? You should also pause to consider issues of **comparability**: will your study have any future importance as a baseline study, and will it be possible to compare your results with those of other researchers, for example at other study sites? These considerations will feed into your planning.

Finally, you should identify what **state variables** (**Chapter 6**), if any, you are aiming to estimate using camera-trapping. This will determine much of the answer to the question of "how" you will do your study (discussed in the rest of **Chapter 7**). Many camera-trapping studies involve the formal estimation of state variables of one kind or another, but some don't. For example, studies of behaviour may use simple mean statistics, such as fruit removal rate (Prasad *et al.* 2010), mineral lick visitation rate (Matsuda *et al.* 2015), or deer vigilance rate (Schuttler *et al.* 2017). Relative abundance indices (**Chapter 6-3-1**) are also not formal state variables. Such studies may not involve complicated statistical analyses, but the application of sound survey design principles (**Chapter 7-3**) is no less essential.

Further reading: Yoccoz *et al.* (2001) discuss the "what" and "why" (as well as the "how") of biodiversity monitoring; Legg & Nagy (2006) discuss ways of making sure that any monitoring programme is well-designed from the outset.

7-2 Broad types of camera-trapping study

Once you have identified your study aims, it may be helpful to consider the broad types of camera-trapping study that exist and how they are related (**Fig. 7-1**). Your study will probably fit into one, or possibly more, of these broad study types. Note that abundance estimation using the Royle-Nichols model (**Chapter 6-3-2**) is best done using an occupancy sampling design. Mark-resight models have been poorly explored with camera trap data to date, but the appropriate methods are similar to those for capture-recapture (see **Chapters 6-3-2** and **6-4-3** for example studies).

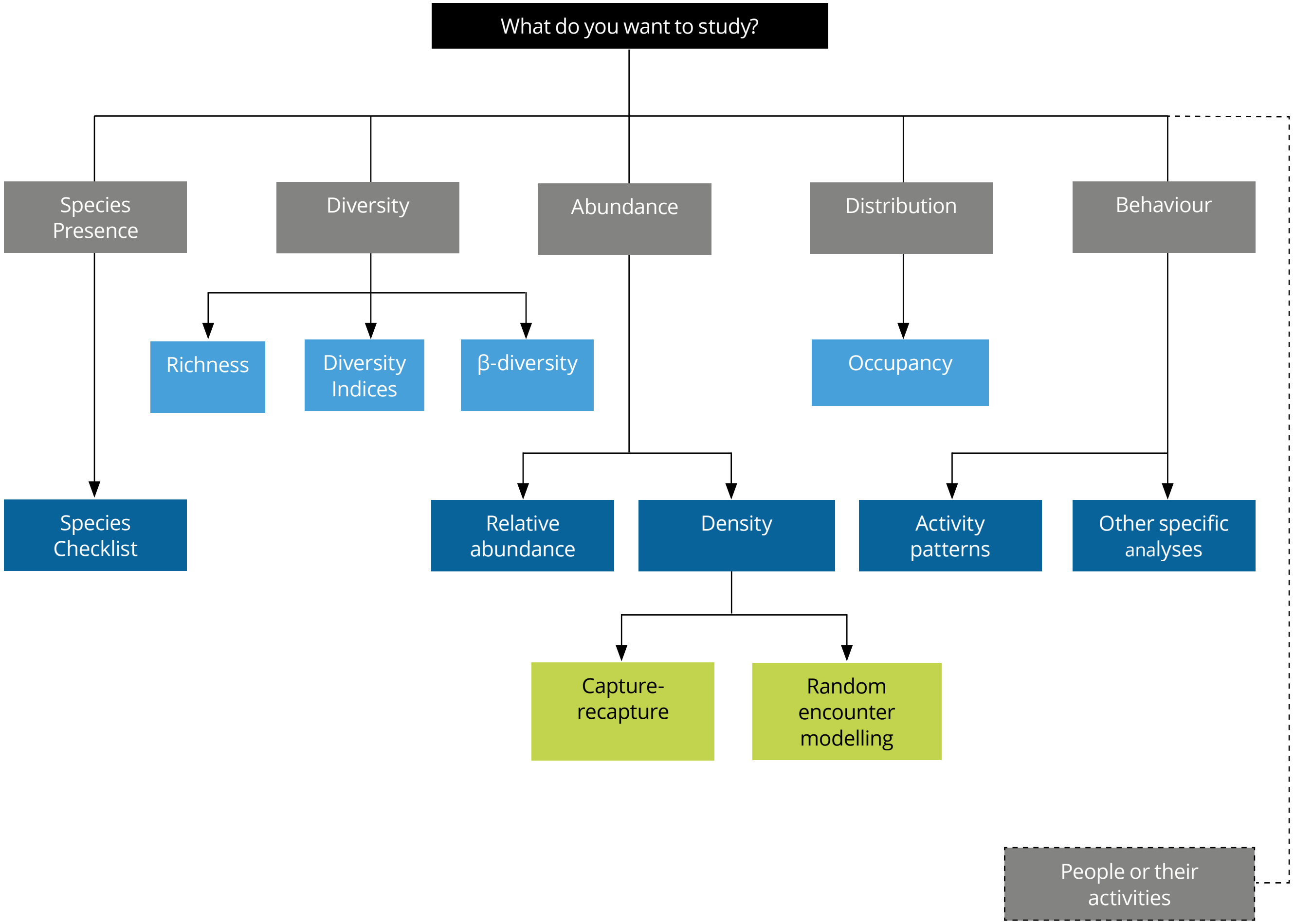


Figure 7-1. Classification of camera trap studies, based on their aims (show in grey) and outputs (show in blue colours). Broad study types are shown in red, for which we provide recommended survey designs **(Chapters 7-4** to **7-11**). An output of animal density can be achieved using two contrasting methods – capture-recapture and random encounter modelling – which are shown separately. Absolute abundance estimation (e.g. using the Royle-Nichols model) has been omitted for simplicity. Camera traps can also be used to gain an understanding of human interactions with the environment. This type of study is shown in dashed outline because, in many cases, the questions are the same as those for studies of wildlife (e.g. presence, distribution, or behaviour), and the same survey design principles often apply (see **Chapter 7-11** for more information).

In the following Chapters, we first provide an overview of general survey design principles, and then give specific guidelines on sampling design and camera deployment for each broad type of camera-trapping study. Note that your own study may be a hybrid of two or more of these types, and you may need to make compromises in order to achieve all of your aims. In such cases, there may be **no simple "right answer"** for the best approach, and small pilot studies or simulation exercises are likely to be especially helpful.

7-3 General survey design principles

You might be forgiven for thinking, if you read many camera-trapping protocols in the literature, that camera-trappers have somehow escaped the statistical constraints placed on everyone else working in ecology. In particular, the central tenet of sampling theory – that a **representative sample** must be taken – is widely flouted in camera-trapping studies. That this is the case, is probably for historical reasons. Camera traps really became a recognised scientific tool when they were combined with capture-recapture methods (e.g. Karanth 1995; Karanth & Nichols 1998), and the methods used in these early studies – placing cameras along conduits of animal movement, such as roads and trails – have stuck. This is more acceptable if robust statistical methods, such as capture-recapture or occupancy estimation, are to be applied to the data, since these methods are able to explicitly control for detectability. However, it much reduces the usefulness of the data for other purposes, such as for diversity estimation, or for monitoring non-target species using relative abundance indices.

The starting point for any sampling design should always be the standard methods applied across the rest of ecology. This includes: 1) the **random** selection of sampling units; 2) **replication** with independent sampling units, and 3) **stratification** according to Chapters of a study area (strata) which are clearly distinct (e.g. habitat types). Sampling effort can be allocated equally across strata, or allocated according to each stratum according to its prevalence in the study area. In the former case, a weighted average of the state variable estimates for each stratum is necessary to recover an overall estimate for the study area, should this be needed.

Sample units can be selected at random using a **simple random** design (e.g. using random grid coordinates) or a **systematic random** design (where sampling locations are arranged in a regular pattern, such as a grid or checkerboard pattern). All else being equal, a systematic random design will yield more precise estimates of state variables than a simple random design, because the variance in detection probabilities and abundance counts across sampling points will be lower.

A **clustered random** design can also be used (e.g. O'Brien *et al.* 2003; Fuller *et al.* 2016; Wearn *et al.* 2016), which may be a more efficient sampling design where accessibility is difficult (Gálvez *et al.* 2016), because multiple cameras can be deployed quickly once a cluster has been reached. In this case, cluster centres are located at random, and then sample units within each cluster are also located at random. Since sampling points within a cluster will be more similar to each other than points between clusters, this sampling design may however demand more complicated analyses (e.g. using random effects) or require that data is pooled across units within each cluster. As for simple random designs, clustered designs will usually yield less precise estimates of state variables compared to a systematic random design, due to the higher variance.

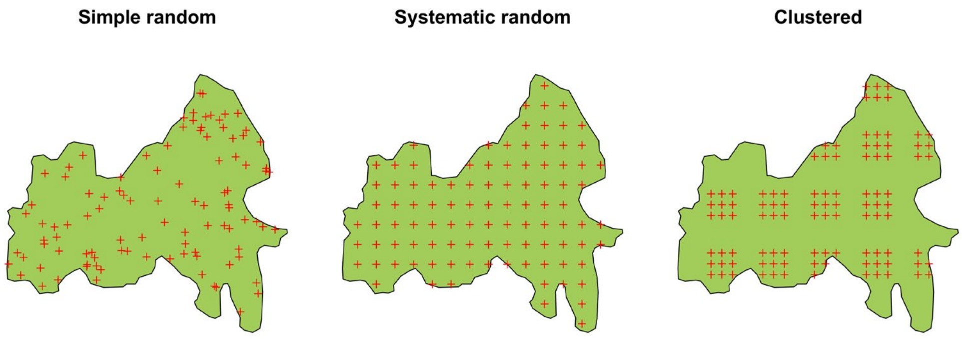


Figure 7-2. Basic sampling designs for camera-trapping. In general, systematic random sampling is preferred, but simple random or clustered designs are useful in some circumstances. Sampling designs for a hypothetical study area (in green) were generated using the "secr" package in R, by adapting code from Mike Meredith. This package has a number of useful functions for automatically creating sampling points.

If the aim of the study is to answer a specific ecological question (i.e. test a hypothesis) rather than simply estimate state variables of interest, then principles of **experimental design** will also have to be employed. The gold standard in such experiments is the **"before-after control-impact"** (BACI) design, which involves submitting half your experimental units to a treatment and leaving the other half as "control" units. True manipulative experiments like this can rarely be done at sufficient scale in ecology, and so natural variation in a factor of interest (e.g. habitat characteristics) is usually exploited instead, in a sort of **"natural" experiment** (sometimes called a "mensurative" experiment). Natural experiments can be a powerful way of making ecological inferences at large spatial scales, but there is an ever-present danger that comes with them: **confounding variables**. Confounding variables can undermine natural experiments and lead to poor or, even worse, wrong inferences about a study system (McGarigal & Cushman 2002). All experiments, whether manipulative or natural, also come with the risk of being **pseudo-replicated** (Hurlbert 1984). Pseudo-replication can sometimes be difficult to diagnose, but can seriously limit the strength of the conclusions that can be drawn from a given study design (Ramage *et al.* 2013).

If you are convinced that you will be able to use a robust statistical method, such as capture-recapture or occupancy estimation, it may be possible to depart from the sampling designs stipulated by basic sampling theory. But if you begin on this journey, you should be fully aware of the **assumptions** of the methods you will be using (see relevant Chapters below), and that you may be more limited in the range of inferences you can make from your final dataset.

Further reading: We point the reader to any textbook on ecological field techniques to learn more about basic sampling theory and experimental design (e.g. Williams *et al*. 2002; Ellison & Gotelli 2004; Sutherland 2006), which is beyond the scope of these guidelines.

7-4 Species check-lists or inventories

7-4-1 Assumptions

Inventory studies, for example rapid assessment surveys, simply attempt to discover what species are present in a given area at a given point in time, and make no attempt to quantify any aspect of communities or populations. **No formal modelling process** is applied and, as a result, no assumptions are explicitly made. For these reasons, check-lists should only ever be considered as **unfinished, working drafts**. For proper inference about how many species exist in an area, or whether an undetected species of interest might actually be present, a formal modelling process must be applied (often requiring more data than are collected during rapid assessments).

7-4-2 Spatial configuration of sampling points

Ideally, standard principles of sampling design should be applied, including randomisation, replication and stratification (**Chapter 7-3**). This greatly increases the usefulness of the data for other purposes beyond check-listing. However, inventory work is typically extremely limited in time and resources (e.g. using just 1-10 cameras) and therefore a **targeted, non-random deployment** of cameras is often justified. In addition, since no model is technically being applied, no assumptions have to be satisfied, so there is total flexibility in how cameras are deployed. For example, if you are tasked with quickly finding out if a riparian species, such as the flat-headed cat (*Prionailurus planiceps*), occurs in a particular area, perhaps because the area is under threat from development, then it would make sense to deploy cameras strategically along water courses and other areas which the species is known to frequent (Wilting *et al*. 2010a). Of course, if you know nothing about the habitat preferences of your target species, it makes sense to deploy cameras in a range of microhabitats or indeed using a random design (e.g. Wearn *et al*. 2013). A random design will stop you from making unintended assumptions about how the target species "views" the given landscape and will result in you sampling all microhabitats in proportion to their availability.

7-4-3 Number of sampling locations

Since no formal modelling is being done, there is **no minimum number of locations** that must be sampled. Of course, the more sampling locations that can be sampled the better.

Given the limited time and resources available to most inventory studies, the number of locations that are sampled in an inventory study will end up crucially depending on how much sampling effort is allocated to each one. For example, with 10 cameras and 4 weeks, it is possible to either sample 40 locations for a week each, or just 10 locations for the full 4 weeks. Different strategies are recommended depending on whether the focus is broad-spectrum sampling of many species, or focussed sampling of one or a few species (**Chapter 7-4-4; Fig. 7-3**). In practice, because of the constraints typically placed on inventory studies, fewer than 20 locations are often sampled.

7-4-4 Number of camera trap nights at each sampling point

In principle, there is complete **flexibility on the number of trap nights** that camera traps are deployed for in an inventory study. However, for broad-spectrum sampling of a wide range of species, it makes sense to sample for a shorter amount of time (e.g. 1-2 weeks) and move cameras to new locations relatively frequently. This will maximise the number of different microhabitats sampled in a short space of time.

If you are targeting a single species, the likely probability of detecting it (for example, based on previous studies elsewhere) can inform your decision. If the detection probability is high (for example, perhaps the species has a small range and is likely to visit your camera trap within a short amount of time), deployment times may be short (e.g. 1-2 weeks). For rare and wide-ranging species (such as big cats), deployment times may need to be much longer (e.g. 2-6 weeks) to ensure a reasonable (better than 50:50) chance of detection. In the latter case, it probably makes no difference if you move cameras frequently or leave them in place for the duration of the short survey time available; whether you detect the species will depend primarily on your ability to identify good locations for your cameras (and on a generous helping of luck). The benefits of leaving cameras in place are that disturbance to sampled sites will be lower (some species may detect your smell weeks after you have been there), but there is a higher risk that cameras might malfunction or run out of battery/memory without you knowing.

7-4-5 Length of study

There is **no minimum time** required for an inventory, but the checklist will become more comprehensive with additional sampling effort. Inventories may take the form of rapid assessment surveys, in which case they may be as short as 1-4 weeks, or they may consist of ad-hoc sampling of an area over a long period of time, possibly multiple years.

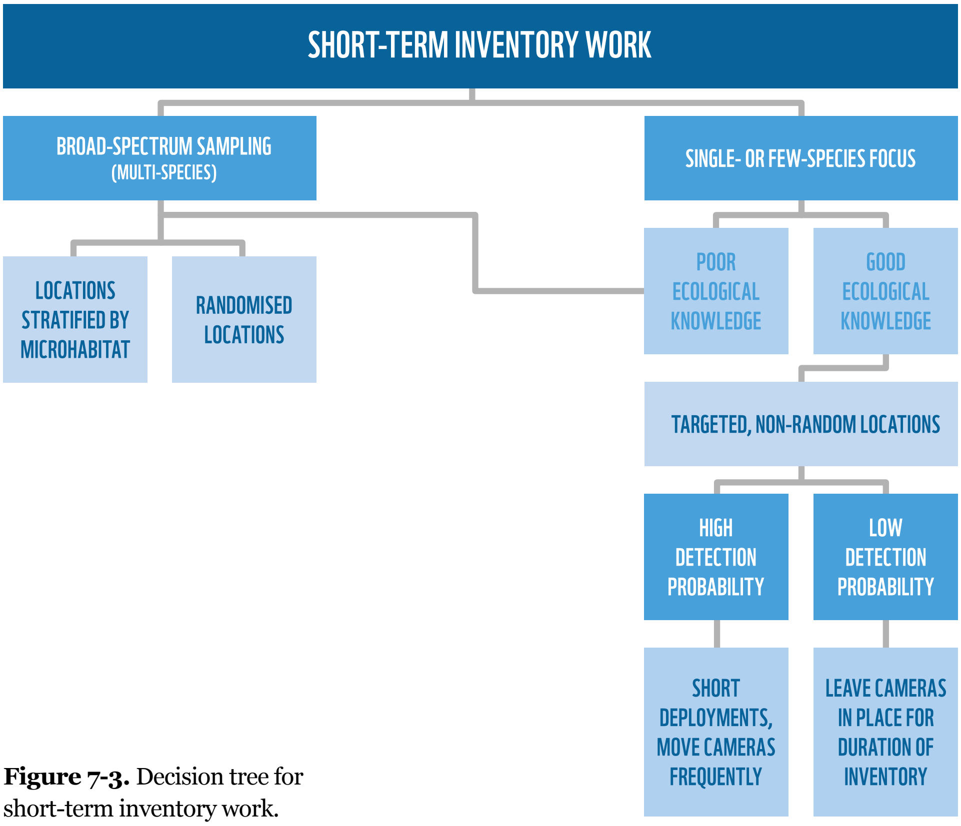


Figure 7-3. Decision tree for short-term inventory work.

7-5 Species richness and diversity

7-5-1 Assumptions

Observed species richness is a biased measure of true species richness (see **Chapter 6-1**). If comparisons are to be made across space or time, the **sampling effort** (e.g. number of camera trap nights) must be comparable. In addition, comparisons of observed species richness assume that the **detectability of each species** has also remained the same, which is very difficult to control if abundance varies (which it frequently will). For this reason, there is not a survey design that can easily be recommended for comparing observed species richness.

There are a number of different approaches for estimating true species richness (**Chapter 6-1**), each with a specific set of assumptions. In addition, indices of species diversity and β-diversity also come in many different forms. However, the most important assumptions are (unsurprisingly) those of **randomness** and **independence**. For analyses which use "sample-based" datasets (the presence and absence of different species across sampling locations), samples are assumed to have been taken at random from the broader population of sites, and assumed to be independent from one another. For "individual-based" datasets (the number of individuals recorded of each species across sampling locations), individuals are assumed to have been sampled randomly and independently. In other words, standard sampling design principles (**Chapter 7-3**) apply in both cases. For the occupancy-based approaches to estimating species richness, **it is possible to relax these constraints** to some degree, because these models provide an opportunity to explicitly describe some of the observation processes at work in a particular study (see **Chapter 7-9** for recommended sampling designs for occupancy).

7-5-2 Spatial configuration of sampling points

It is strongly recommended that standard principles of sampling design are employed when attempting to estimate species richness or diversity, including randomisation, replication and stratification (**Chapter 7-3**). **Randomisation**, in particular, is something which has often been overlooked in camera-trapping studies, with many studies only placing cameras along trails. If locations are chosen non-randomly there is a high likelihood that some habitats, and therefore some species, are missed entirely. Whilst camera traps are already limited in the subset of species they sample (for example, they do not sample species too small to trigger their sensors), it is best not to introduce additional complications caused by subjective decisions about camera placement. Doing so, runs the risk of reducing the **comparability of the results**, across space and (if cameras stations are not fixed) across time. Non-parametric estimators of species richness and diversity likely already deal rather poorly with the **heterogeneity in species detection probabilities** that is common in camera-trapping studies, and introducing additional complexity into this mix, by altering camera placement, is likely to introduce even more bias.

Occupancy-based approaches to estimating species richness may better account for differences in camera placement strategies, because detection probabilities are explicitly incorporated into the model. However, even these models may not succeed if camera placement strategy effectively reduces the detection probability of a species to zero. Random placement of cameras, or at the least placement of some cameras **"off-trail"**, will ensure that all species in a community have a reasonable chance of detection.

Samples for estimating richness and diversity should also be **independent**, which technically means that any two locations should not be sampling the same community of animals. Note that this may be hard to achieve when considering the movement distances of some species, such as big cats, and in practice an inter-trap distance of 1-2 km is often used (e.g. Tobler *et al.* 2008; Ahumada *et al.* 2011; Kinnaird & O'Brien 2012).

In a study in the Peruvian Amazon, no difference in observed richness was found when trap spacing was varied from 1 to 2 km (Tobler *et al.* 2008). Note that the importance of ensuring absolute independence between cameras is often overstated, and may have little effect on statistical inference (see **Box 7-1**). In any case, it is possible to statistically account for dependence between camera samples (e.g. using mixed-effects models or by explicitly including an autocorrelation structure in the model), so all is not usually lost.

Finally, the well-known species-area relationship tells us that our estimate of species richness is dependent on **sampling area**. As we increase the area enclosed by a camera grid, for example, we might expect species richness to increase. This tells us that we should not compare richness or diversity estimates between studies with different grid sizes. In reality, if habitat is uniform, or if camera traps are to some degree sampling the same animals (e.g. if traps are placed close together), we may not see this pattern over relatively modest changes in grid size. For example, in the Peruvian Amazon, Tobler *et al.* (2008) did not see any difference in observed richness when they increased grid size from 15 to 50 km^2. We suggest that comparisons between studies with approximately the same grid size are probably allowable, although greater investigation into this is warranted.

7-5-3 Number of sampling locations

There are no hard-and-fast rules for the number of sampling locations required to estimate the species richness or diversity of a local area, such as a national park, but it seems unlikely that a decent sample could be obtained with less than 20 locations, and **50 locations might be a better target**. If you want to stratify your richness or diversity estimates, for example by habitat, you will need 20-50 locations per stratum. The target number of locations for any given study will, in reality, depend on a large number of factors, including:

- Size of the study area (large areas will require more locations)
- β-diversity (lower community variance means more locations are needed)
- Spatial layout of cameras (if some of the cameras are clustered together, they might be sampling more similar habitats, and so more locations are needed)
- Number of trap nights each point is sampled for (fewer trap nights per point means more locations are required)

The few species-accumulation curves for camera trap data that have been published seem to level off between 20 and 100 locations (Ahumada *et al.* 2011; Li *et al.* 2012; Wearn *et al.* 2016). Helpfully, it may not always be necessary to sample until species-accumulation curves have begun to reach their asymptote. Non-parametric methods of estimating asymptotic richness are thought to yield good results even when **extrapolating to double or triple the size of the sample** (Colwell *et al.* 2012). Occupancy models may be even more forgiving, since the observation process model is more sophisticated (especially for multi-species occupancy models), but this is yet to be shown empirically.

7-5-4: Number of camera trap nights at each sampling point

As with the number of sampling points, there are no concrete rules on the number of trap nights required per sampling point. The required number will depend on, for example, animal abundance (low abundance means few detections are made and more trap nights are needed) and community evenness (a large number of rare species in the community means more trap nights are needed to allow them all a chance of visiting a camera location). However, a commonly used target is **30 trap nights per location** (Ahumada *et al.* 2011). This appears to be a reasonable recommendation for a diverse community with some very rare species. If diversity is very low, 1-2 weeks of sampling per location may be sufficient.

Note, that the aim is not usually to record every species at every sampling location, but instead to adequately sample the community at the scale of the trapping grid. The best way to do this is to **sample more locations for a shorter period**, rather than to sample just a few locations for a very long period (Si *et al.* 2014). If you really want to capture all species using a given sampling location, significantly longer sampling efforts will be required (e.g. Si *et al.* 2014).

7-5-5 Length of study

The required total sampling effort will be a multiplication of the required number of locations (20-50; **Chapter 7-5-3**) and required number of trap nights at each location (30; **Chapter 7-5-4**). This gives a range from 600 to 1,500 trap nights, which more-or-less agrees with the range of recommendations that have been made across specific camera-trapping studies. For example, Si *et al.* (2014) recommended a survey of at least 931 trap nights to detect 90% of the common species in a site in eastern China. A target in this ball-park has also been recommended for a reasonable chance of detecting rare species, such as tigers (1,000 trap nights; Carbone *et al.* 2001), cat species in Borneo (700-2,800 trap nights; Wearn *et al.* 2013), and all but the most infrequently detected Amazonian mammals (~1,500 trap nights; Tobler *et al.* 2008).

As a general recommendation, we suggest that diversity studies should be **at least 1,000 trap nights.** This should not be difficult to achieve in most cases, and the majority of contemporary camera-trapping studies already exceed this. For recent camera trap studies (in the period 2008-2013), the median sampling effort across 266 camera trap studies was 2,055 trap nights (Burton *et al.* 2015). As camera trap technology improves (in particular battery life and memory capacity), typical camera-trapping sampling efforts will increase even further.

In order to make estimates of richness and diversity that make sense, it is necessary to collect data over a short enough period such that these state variables do not change over the course of the study. For nonparametric estimators of richness, there are the added assumptions that, for sample- and individual-based approaches, species composition and abundance do not change, respectively. In other words, the **community is considered to be "closed" to changes**, an assumption which has parallels in occupancy (which assumes distributions are "closed"; **Chapter 7-9**) and capture-recapture (which assumes populations are "closed"; **Chapter 7-7**). In practice, there is only a poor understanding of how quickly changes in richness, composition and abundance can occur. In studies of birds, evidence was found for changes in occupancy on the order of 1-3 weeks (Rota *et al.* 2009). For the medium- and large-sized mammals typical of camera-trapping studies, an assumption of a **3-6 month period** of community closure seems reasonable in the absence of empirical data. If your site is highly seasonal, you will need to think carefully about the best time to sample, for example at a time of year when territories are relatively stable (studies of birds typically choose the breeding season).

By analogy with occupancy and capture-recapture models (Kendall 1999; MacKenzie *et al.* 2006), violations of community closure may not actually introduce large bias into richness estimates if changes in composition occur at random. This means survey durations of more than 6 months might be defensible in some cases. If you think communities in your study are changing over time, for example due to extinction debt or due to continued anthropogenic threats, then you will have to think carefully whether you will be able to sample all your sites in a short enough time window to make an estimate which is sensible and useful.

BOX 7-1: ARE YOUR CAMERA TRAP LOCATIONS INDEPENDENT?

This is a tricky question, and can be approached from two angles. From a practical point of view, we can determine if our camera traps are independent, in the sense of **not sharing any animals**, by conducting radio- or GPS-tracking studies and estimating **home-range sizes**. If our camera traps are further apart than a home-range radius, then they can be considered to be independent. This information is important, in particular, if we are using **occupancy models**, since it helps us decide whether to interpret our estimates as “probability of occupancy” or “probability of use” (**Chapter 6-5**).

However, another point of view is **statistical independence**. We are typically interested in the question of whether our camera traps are independent or not because we are worried about **pseudo-replication**. Pseudo-replicates are samples which are not truly independent and can lead to confidence intervals around an estimate of a state variable – such as mean species richness or mean trapping rate – which are biased too small. Non-independence can also cause non-parametric species richness estimators to underestimate species richness. These biases arise when species are significantly clumped in space. Importantly, this clumping has been found to be weak in camera-trapping data when it has been looked for (e.g. Kays *et al*. 2011; Wearn 2015). This suggests that, though there are strong theoretical reasons to expect clumping and autocorrelation, it may be such a weak signal that it has **little effect on statistical inference** in practice.

There are cases where we **deliberately want dependence** among our camera traps. For example conventional capture-recapture methods require that there are no “holes” in trapping grids where an animal could be missed entirely, which can be achieved by making sure that camera trap locations are sufficiently close together. Spatially-explicit capture-recapture and mark-resight methods also require that individual animals are captured at more than one camera trap location (ideally, many), and in fact the recommendation is to place multiple camera traps per home-range (**Chapter 7-7-2)**.

7-6: Relative abundance

7-6-1: Assumptions

It is sometimes stated in the literature that the use of raw trapping rates, i.e. relative abundance indices, requires fewer modelling assumptions. This might be because simple statistical approaches (such as t-tests and linear regressions) are often applied to relative abundance data. In fact, **a large number of assumptions must hold** if relative abundance indices are to yield useful information about variation in actual animal abundance across space, time and species. As with observed species richness, it is therefore difficult to recommend a survey design which will allow for robust inferences using relative abundance indices. Given the ubiquity with which indices are used, we nonetheless offer some recommendations which will at the least help to moderate some of the problems with them.

Given all of the potential variables that can affect relative abundance indices, it is essential that as much of the methods and sampling design are as **standardised** as possible (over space and-or time, depending on how the indices will be used in comparisons). In particular, it is critical to obey standard principles of sampling design (**Chapter 7-3**). Field methods should also be consistent. A simple example of this is that relative abundance indices should only be compared across similar camera models, ideally with the exact same sensor. This is because different sensors often have markedly different detection zone sizes, which affects detection probability. It is possible, in principle, to control for variation in detection distances (i.e. the radius of detection zones), but this requires placing markers in the field of view of the camera (**Chapter 6-3-1**). We recommend other ways of standardising the methods and sampling design in the Chapters below.

7-6-2: Spatial configuration of sampling points

To minimise the comparability issues with relative abundance indices, it is strongly recommended that standard principles of sampling design are employed, including randomisation, replication and stratification (**Chapter 7-3**). **Randomisation** can be achieved with a systematic (e.g. a grid) or simple random (e.g. random coordinates) design, with cameras deployed as close to the random points as reasonably possible (see **Chapter 7-8-2** for further guidance on this). Randomisation has often been overlooked in camera-trapping studies of abundance, as it has been in richness and diversity studies also. Consider the typical placement strategy of targeting locations with high animal activity, such as along trails. Even if all species have a chance of being detected (this is unlikely to be the case), it should be clear that the relative abundance indices for each species will be a function not just of their abundance, but also of how strongly they prefer walking along trails. This interaction between how animals use a habitat and the specific placement strategy used can lead to a biased view of relative abundance (Wearn *et al.* 2013). Even if comparisons are only made within a species, for example across space or time, there is still the problem that animals may alter their preferences for trails across space and time. Whether relative abundance indices are used for comparisons across space, time or species, it is clear that a random placement strategy must be used.

The recommended inter-trap distance for relative abundance indices depends on the type of analysis that will be conducted. If the trapping rate from each camera point is to be treated as a data point (for example, in a statistical test), then samples should also be independent. In this case, the typical **inter-trap distance of 1-2 km** should ideally be used (although see **Box 7-1**). Models which account for the non-independence can be used if necessary (e.g. generalised least squares, or mixed-effects models). If trapping rates are to be calculated over an array of random cameras (for example, for comparing across study sites), then the independence among points is arguably less of an issue, as samples can be thought of as taking **random point measurements** of a continuously-varying density surface.

7-6-3: Number of sampling locations

There are no hard-and-fast rules for the number of sampling locations required to obtain a reasonably precise relative abundance index (as was the case for richness and diversity). In principle, sampling one or two random locations will provide an unbiased estimate of the index, but the precision of the index will not be known (for one location) or will be very large (for two locations). Sampling **more locations increases the precision** of the relative abundance index estimate and provides more statistical power with which to make comparisons across space or time.

The number of locations required for a reasonably precise estimate depends on how patchy the species is, and therefore how variable the trapping rates across locations are. Simulations have shown that, if variance in trapping rates across locations is high (this will be the case for almost all species), precision is much improved by sampling at least 20 locations, and **ideally more than 50 locations** (Rowcliffe *et al.* 2008). If you want to model indices as a function of covariates, you will need a larger sample still (perhaps 20-50 locations per covariate). The variance in trapping rates will also be higher if locations are only sampled for a low number of trap nights, or if cameras are deployed in clusters. In both cases, more sampling locations will be required to obtain a given precision.

7-6-4 Number of camera trap nights at each sampling point

In principle, there is **no minimum number of trap nights** required per sampling point for calculating a relative abundance index, but it will be estimated with greater precision if it is based on a larger number of trap nights. If spatial patterns in relative abundance are of interest, sampling effort should also be sufficient to **capture the variation in abundance**; this will not be achieved if the counts across locations are very low (e.g. only varying between 0 and 1). A target of **at least 30 trap nights,** and ideally much longer, per location is probably sensible for most species.

7-6-5 Length of study

For richness and diversity studies, a species just needs to be detected with a reasonable chance, but to assess relative abundance, it should ideally be captured many times. An index should be based on > 10 captures, and **ideally > 20 captures**, in order to be reasonably precise (Rowcliffe *et al.* 2008). For common species, simulations and empirical work suggest that this will be achieved if a study lasts at least 250 trap nights (Rowcliffe *et al.* 2008; Rovero & Marshall 2009). However, for most species significantly larger efforts will be needed. For densities typical of many carnivores (and the rarest ungulates), **at least 2,000 trap nights** will be required to obtain 20 captures (Rowcliffe *et al.* 2008). For “hyper-rare” species (caught only once every 1,000 trap nights), which can form a significant proportion of diverse mammal communities (often 30% of more; O’Brien 2010), more than 20,000 trap nights might be required to obtain sufficient captures.

There is **no formal closure assumption** for relative abundance indices, and the trapping rate will be a reflection of **average abundance** for the period of time over which the index is calculated. However, it makes sense to calculate indices at time intervals of < 1 yr so that they are meaningful and useful, and probably at finer time-scales (< 3 months) if changes in threats or management at a site are occurring rapidly.

7-7 Capture-recapture

7-7-1 Assumptions

Capture-recapture models, whether conventional (non-spatial) or spatially-explicit, come with a host of assumptions. Some of these assumptions have been explored using simulations and empirical work, especially for the conventional capture-recapture models. However, it is worth noting that these methods were developed in the context of high density species with small ranges (such as mice). Their application to camera-trapping, typically of low density species with very large ranges (such as big cats), is still poorly-explored in comparison.

The key assumptions of capture-recapture models are:

1. Individuals **do not lose their marks or are misidentified**
2. All animals have an **equal probability of capture** (or, for spatially-explicit models, an equal probability of capture for a given distance from the centre of their home range)
3. **Captures of different individuals are independent** (hence why most studies exclude dependent young)
4. **No behavioural response** to being trapped or marked
5. Sampling **occasions are independent**
6. Population is **demographically closed**, i.e. no births or deaths (and, for conventional models, **geographically closed**, i.e. no immigration or emigration).

Some of these **assumptions can be relaxed** to some degree using more sophisticated models, but such models are usually more demanding in terms of the amount of data required. **Heterogeneous capture probabilities** (violation of assumption 2) are especially problematic for capture-recapture models, especially when the number of individuals in the sample is < 50 (Harmsen *et al.* 2011), as is common in camera-trapping studies. Assumptions 1 and 3 are less of a nuisance for camera-trapping studies, which usually just rely on natural markings to identify individual animals, but behavioural responses to some types of cameras (violation of assumption 4) can be significant (e.g. Wegge *et al.* 2004).

Spatially-explicit models come with **additional assumptions about animal movement** (Borchers & Efford 2008; Royle *et al.* 2009b; O'Brien & Kinnaird 2011).

These include:

1. Animal **ranges are stable** throughout a trapping session
2. Captures do not affect subsequent **patterns of movement**
3. **Trap placement** is random with respect to the distribution and orientation of animal ranges
4. **Home range centres** are distributed according to a Poisson distribution, or other defined distribution such as negative-binomial

7-7-2 Spatial configuration of sampling points

Since capture-recapture is based on the repeated detection of individual animals, it is imperative that animals can actually be told apart (assumption 1), and this is not always easy from grainy, blurry or black-and-white camera trap images. As a result, some thought needs to be put into how exactly camera traps will be set up (**Chapter 10-4**), as well as their required specifications (**Chapter 8-2**). From a survey design point-of-view, a key consideration is whether **paired cameras** will be used (see **Box 7-2**).

Since capture-recapture models explicitly model detection probability, in theory there is much more **flexibility on where cameras can be placed.** Most studies therefore target roads, trails and other focal points for the given species. However, assumption 2 – that all animals have an equal probability of detection – can be violated if different classes within the population do not all have the same microhabitat preferences. For example, capture-recapture studies of big cats, which almost always place their cameras on trails, often report finding more males than females (e.g. Silver *et al.* 2004; Sollmann *et al.* 2011, 2014; Cheyne *et al.* 2013; Tobler *et al.* 2013). This has been suggested to be because of the **different preferences for trails** among males and females (Foster & Harmsen 2012; Gray & Prum 2012; Wearn *et al.* 2013). Using a random placement design, it was shown that male Sunda clouded leopards (*Neofelis diardi*) prefer walking along logging roads, whilst females (which often have cubs, vulnerable to infanticide) prefer to use dense vegetation away from roads and trails (Wearn *et al.* 2013). Similarly, male jaguars (*Panthera onca*) have been shown to dominate the use of wide trails in dense forest habitat, with females instead seeming to use small waterways to move around (Foster *et al.* 2010). Similar differences in microhabitat use can exist across age and social status classes, as has been found for coyotes, *Canis latrans* (Larrucea *et al.* 2007).

Randomised placement of cameras or, at the least, **placement of cameras in a range of microhabitats** (in particular, not all on trails), will help to reduce the heterogeneity in detection probability across individuals. This may reduce the total number of detections in the dataset, but ultimately lead to more accurate inferences about the population size. If there are sufficient detections in the dataset, different classes of individual within the population can also be modelled separately. Randomised placement will also help to satisfy the additional assumptions that come with spatially-explicit capture recapture, that cameras are placed randomly with respect to the distribution and orientation of home ranges. In particular, placing cameras preferentially in areas of unusually high density may lead to biased inferences with respect to the broader study area.

For capture-recapture, unlike the survey designs considered above, **camera locations should be sufficiently close to one another** such that individuals are picked up across more than one location. In other words, dependence between cameras is specifically wanted. This is particularly the case for SECR, which models the decline in capture probability with increasing distance from an animal's home range centre. As a result, cameras should be spaced apart by less than a home-range radius for SECR modelling, and ideally considerably less. Simulations suggest that accurate results will be obtained if cameras are spaced apart by a maximum of 0.8 times an average home-range radius (Sollmann *et al.* 2012; Sun *et al.* 2014). However, for reasonably precise estimates, a good recommendation is to aim for **one third of a home-range radius** (Sollmann *et al.* 2012). This radius provides a good balance between trapping grid size (which should be as large as possible) and trap spacing (which should be as narrow as possible, all else being equal). This suggests that ~4-7 cameras should be placed in each home-range.

For conventional capture-recapture, cameras must be spaced apart by less than one home-range diameter to **ensure that there are no "gaps" in the trapping grid** (remembering assumption 2). Conventional capture-recapture does not require that individuals are caught at more than one location, but aiming for this does ensure that there are no gaps in the trapping grid. As a result, a good recommendation is actually to aim for at least 4 cameras per home range (White *et al.* 1982; Dillon & Kelly 2008). Note that this recommendation is similar to that for SECR modelling.

BOX 7-2: SHOULD SINGLE OR PAIRED CAMERA TRAPS BE USED IN A CAPTURE-RECAPTURE STUDY?

For a capture-recapture survey, camera traps can be set up singly as normal, or on either side of a trail (slightly offset, so that the flash on each camera does not interfere with the opposing camera) to obtain **images of both sides of an animal**. Using paired cameras will often give you a much **higher chance of recognising all individuals** captured in a survey, irrespective of which direction they approach cameras from. Using two cameras also **decreases the chances of missing captures** entirely (Tobler *et al.* 2008).

Figure 7-4. Example of a paired camera trap setup used in a capture-recapture survey of Malayan tigers (*Panthera tigris jacksoni)*. The opposing camera trap – seen in the background (inside dotted line) – was set up with an offset to avoid interference due to the flashes. Image © Christopher Wong/WWF-Malaysia.

For a given budget, a paired camera design can only sample **half the number of locations** that a single camera design can. **Single cameras can sometimes be effective for identifying individuals** if they are able to take lots of images of each individual, for example if they are set to near-video or video modes, or if animals remain in front of cameras for an extended period of time (as may happen if baits or lures are used). Using these approaches, some examples do exist of density estimation from single cameras (e.g. Watts *et al.* 2008; Royle *et al.* 2011; Du Preez *et al.* 2014; Alexander *et al.* 2015).

BOX 7.2 CONTINUED...

Images from outside the formal trapping period can also be used to aid identification, as can photographs from direct observations (e.g. Karanth, 1995). With single camera surveys, quite a few captures may not be identifiable (as can happen in paired camera survey as well), which is accounted for with a **lower mean capture probability**. However, biased estimates of density will be obtained if some individuals in the population have a much lower chance of being positively identified (such as those on the edge of the trapping grid, which are caught fewer times).

New statistical methods promise to increase the effectiveness of single camera designs, by allowing information from multiple marks (e.g. images of the left and right side of animals) to be integrated into a single capture-recapture model (McClintock et al. 2013; Augustine et al. 2016). It is also possible, in principle, to estimate density **using data from just one side of each animal** (e.g. O'Brien *et al.* 2003; Thorn *et al.* 2009), but after filtering the dataset there is a risk that the number of individuals remaining, and the overall capture probability, might be too low to allow a formal density estimate.

If the primary aim of your study is to estimate the density of an individually-identifiable species, then **paired cameras are the default option in most cases.** However, if you also have broader aims for your camera-trapping study, such as estimating the occupancy of a range of different species, then it will also be worth considering if a single camera design will be viable and satisfy multiple aims.

Figure 7-5. Identifying snow leopards using single cameras, based on their facial pelage characteristics. Panels **B** and **C** show images of the same individual, whilst panel **A** shows a different individual. Figure from Alexander *et al.* (2015).

Another consideration with respect to the spatial layout of cameras is the shape of the trapping grid. For other camera-trapping study types (e.g. diversity estimation, random encounter modelling and occupancy), the shape of the sampling design per se is not important, only the requirement for a random (and possibly stratified) sample of the area of interest. For conventional capture-recapture, however, the **grid should be as compact as possible**, with a low surface-to-area ratio. This is to minimise the number of "edge" animals, which are infrequently recaptured and cause heterogeneity in capture probabilities. Reducing edge effects will also improve the estimation of home-range diameters based on the MMDM. A circle would be the best shape to accomplish this, but a square or rectangle is most often used, possibly due to the difficulties associated with setting up a circular design. Bondrup-Nielsen (1983) found, using simulations, that rectangular trapping grids needed to be at least 16 times the home-range of the species to minimise these edge effects, which will be difficult to achieve in most cases. More achievable is the recommendation by Maffei & Noss (2008), based on field data, that the area covered by a **trapping grid is at least 4 times the average home range size** of the species in order to obtain reasonably precise estimates of density.

For SECR, variation in capture probabilities between "core" and "edge" animals is accounted for by the model and presents no problem. Since SECR incorporates space, there is in fact great freedom in how cameras are laid out. In general, it has been found that **elongated designs work better for SECR** because this allows for better characterisation of home-range size (Sollmann *et al.* 2012; Tobler & Powell 2013). A simple example of this is the rectangular trapping grid (Tobler & Powell 2013). If animal territories overlap, rectangular grids just the size of a **single home-range can be large enough** to yield accurate density estimates (Sollmann *et al.* 2012). However, if overlap between home-ranges is low (as can happen also in low density populations), it may be necessary to sample an area equivalent to 4 home-ranges (Tobler & Powell 2013), as for conventional capture-recapture.

The important thing to remember for any elongated design is to make sure the **directionality is determined randomly;** it should not align along features that may be determining the orientation of home-ranges (such as rivers or movement corridors). This would lead to poor estimation of animal movement scales and cause severe bias in the density estimates. In principle, it is possible to use transects to estimate density using SECR, which would be an attractive option in study areas which are difficult to traverse. However, given that transects only sample animal movement in one dimension, there is an even higher risk than when using rectangular grids that they might align with the orientation of home-ranges. For this reason, Efford *et al.* (2005) suggested the "hollow grid" (traps arranged in the outline of a square or rectangle) as an efficient and practical design which samples animal movement in multiple directions. We are not aware of any examples of this being used in camera-trapping studies.

The greater freedom that the SECR approach allows, in terms of how cameras are laid out, also opens up the possibility of **clustered designs**. Multiple grids (or even hollow grids) can be deployed across the study area of interest, in order to maximise the number of individuals exposed to sampling, but still adequately sample movement scales. This has been found to be an especially efficient design in simulations (Sun *et al.* 2014). The benefits of using clustered grids must however be balanced with other demands on the sampling design, for example for assessing diversity or occupancy. Clustering introduces additional complexity into the analyses in such cases, which would have to be dealt with (for example, using random effects).

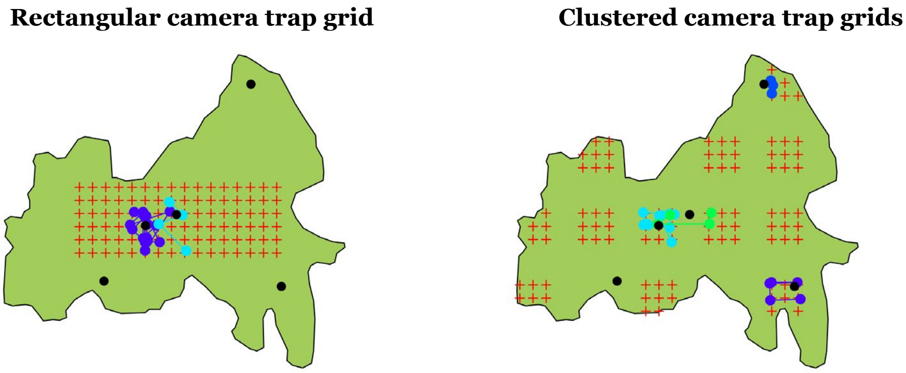


Figure 7-6. Example camera trap sampling designs for spatially-explicit capture-recapture modelling. Here a 16 x 6 rectangular design is compared to a design using a similar number of cameras systematically arranged in 3 x 3 clusters. Activity centres are shown (black dots) for the five animals inside the study area. Data was simulated for a 3 month survey, with captures displayed (blue and green dots). The two designs yielded a similar number of detections (23 and 22), but the clustered design detected 4 of the 5 individuals, compared to just 2 for the rectangular design. By repeating this simulation hundreds of times, it it possible to show that the clustered design gives less biased density estimates. Sampling designs and simulated data were generated using the "secr" package in R, by adapting code from Mike Meredith.

7-7-3 Number of sampling locations

The number of sampling locations determines the number of individuals in the population that are exposed to sampling. Sufficient locations should be sampled to encompass the ranges of **5-10 individuals at a bare minimum**, since models will likely fail to fit if < 5 individuals are captured (Krebs *et al.* 2011; Noss *et al.* 2012; Tobler & Powell 2013). In a review of camera trap capture-recapture studies done in the period 1995-2010, the average number of captured individuals was 13 (Foster & Harmsen 2012). Studies focussing on big cats typically involve even fewer individuals, 8-10 on average (Foster & Harmsen 2012; Tobler & Powell 2013). Whilst this shows that it is possible to obtain density estimates using very small datasets, ideally at least 20 individuals should be sampled (White *et al.* 1982; Foster & Harmsen 2012), in order to obtain a reasonably precise estimate for useful monitoring (e.g. a coefficient of variation < 20%). Modelling success will also depend on obtaining **recaptures for at least some of the sampled animals,** and ideally 20-50 recaptures in total (Efford *et al.* 2004; Noss *et al.* 2012). For SECR, modelling success will additionally depend on recaptures of some animals being made in multiple traps, in order to successfully estimate the scale of movements (Noss *et al.* 2012). Given that it's difficult to predict these various properties of the final dataset, it's a good idea to have some sampled individuals "in reserve", leading to the **overall recommendation to expose 10-30 individuals to sampling** (Karanth *et al.* 2011). If the plan is to model individual covariates (such as age or sex), then it will be necessary to achieve this for each class of individual.

Given this overall sample size recommendation, and the recommendation to place ~4 cameras per home range (**Chapter 7-7-2**), a naïve number of **camera locations to aim for is 40-120**. This assumes no home-range overlap among individuals, and therefore it may be possible to obtain a density estimate using as few as 20 locations, albeit with low precision. Across camera trap capture-recapture studies of jaguars, an average of 30 camera locations were used, with a range of 11-134 (Tobler & Powell 2013). If **capture probabilities are low** (e.g. < 0.1), then **more camera locations** will be needed (60-100; Tobler & Powell 2013), all else being equal, because more cameras will fail to make a capture and more individuals will be missed by the survey.

7-7-4 Number of camera trap nights at each sampling point

For capture-recapture modelling, the number of trap nights at each sampling point determines the number of trapping occasions, which must be > 1. Sampling for more trapping occasions is not, by itself, very helpful for modelling. However, by **pooling data across multiple trap nights** (e.g. defining each occasion as 5 trap nights instead of 1 trap night), it is possible to **increase the capture probability** of the species and, in turn, improve the precision of estimates. This may also help to satisfy the assumption that all captures are independent.

For readily-detectable species, it may be possible to achieve a reasonable capture probability with < 30 trap nights per location (e.g. Bengal tigers, *Panthera tigris*: Wegge *et al.* 2004). However, for most species, more than 30 trap nights will be required if an estimate is to be obtained, and **upwards of 60 trap nights if the estimate is to be reasonably precise** (Tobler & Powell 2013). For very low density species, with **low capture probabilities, 90 or even 120 trap nights** of sampling may be required (Tobler & Powell 2013).

Note that for conventional capture-recapture, it is best to try to keep sampling effort the same across sampling points in a survey, because it is difficult to correct for this during modelling (one crude option is to include the number of trap nights achieved in each sampling occasion as a covariate for detection probability). For spatially-explicit models, it is possible to specify exactly when camera traps were functioning at a given site, and so varying sampling effort presents no problem.

7-7-5 Length of study

Given a recommendation of sampling 40 locations each for 30 trap nights, a ball-park estimate of the number of trap nights needed for a capture-recapture study can be obtained, i.e. **1,200 trap nights**. This is not to say that capture-recapture estimates have not been made on far fewer trap nights, but these estimates will typically have low precision. For **poorly detectable and low density species**, considerably larger efforts will be required, **upwards of 3,600 trap nights** (60 locations for 60 trap nights).

The period over which the study is done should be **as short as possible** in order to satisfy the assumption of **demographic closure**. Typically, though, this is constrained by the resources available. In particular, if the number of camera traps available is fewer than the number of sampling points required, it will be necessary to move cameras around the study area. The length of time that populations can be considered closed likely varies considerably between species, but a period of 2-3 months has typically been used for big cats (e.g. Karanth & Nichols 1998; Silver *et al.* 2004). Capture-recapture methods have also been applied to tiger datasets collected over 6 month (O'Brien *et al.* 2003) or ~12 month (Karanth 1995; Kawanishi & Sunquist 2004) sampling periods, and Tobler & Powell (2013) note that the benefits gained by extending sampling periods should often outweigh the risk of violating closure. In addition, it has been shown that migration of animals in and out of a study area does not necessarily cause bias in conventional capture-recapture models (although it reduces precision), as long as the movements are random and not occurring in one direction (Kendall 1999). It does, however, alter the interpretation of the abundance estimate, from a snapshot estimate of the number of animals within the trapping grid at a given sampling occasion, to the number of animals in the broader **"super-population"** that might use the trapping grid during the study (Kendall 1999).

7-8 Random encounter modelling (REM)

7-8-1 Assumptions

The random encounter model involves the estimation of a number of parameters (**Chapter 6-4-4**), and each of these components of the model come with their own assumptions. These assumptions must be clearly understood from the outset of a study if the method is to be applied correctly, since they have implications for sampling design, camera specifications (**Chapter 8-2**) and how the data is both catalogued and stored (see below and **Box 6-2**).

The most important assumption is that camera traps are placed **randomly with respect to animal movement** (Rowcliffe *et al.* 2013). This assumption has sometimes been interpreted as a requirement for random animal movement (e.g. Linkie *et al.* 2010), but the random encounter model deals well with non-random animal movement, so long as random sampling locations are used (Rowcliffe *et al.* 2013). Consider, for example, a riparian species which only frequents river banks. Monitoring this species by only placing cameras along rivers will give a misleading view of the density of this species, at the scale of the broader landscape (much of which is not riparian habitat). Placing cameras randomly across the landscape will mean that only a subset of cameras will actually sample the riparian habitat, and the density estimate at the scale of the study area will correctly be adjusted downwards. Note that, in practice, species with very restricted distributions in a landscape are best sampled using a stratified design (see **Chapter 7-8-2**).

The random encounter model also assumes that **independent "contacts"** between camera traps and animals (akin to contacts between gas particles) can be accurately counted (Rowcliffe *et al.* 2008). This counting is different to that commonly employed, for example when calculating a relative abundance index (**Box 6-2**). Specifically, successive photographs of a species are deemed to be independent contacts if the animal has **left the camera detection zone** in the period between them, even if only for a very short period of time. If an animal remains in front of a camera for a very long period of time, this is counted as a single contact, as long as the animal does not leave the detection zone.

Other assumptions of the model include: that **animal movement is not affected** by the camera traps, for example with a "trap shy" or "trap happy" response (Rowcliffe *et al.* 2008); that unbiased estimates of **animal activity levels** (the proportion of time animals are available for detection by cameras) and **animal speed** can be obtained (Rowcliffe *et al.* 2014, 2016), and that a camera's detection zone can be approximated well using a **2D cone shape** (technically called a circle segment), defined by the radius and angle parameters (Rowcliffe *et al.* 2011). If activity levels and speed are to be estimated from the camera trap data itself, then at least two further assumptions must be met: that all animals in the population are active at the **daily peak of activity** (Rowcliffe *et al.* 2014), and that **animals moving very quickly** past a camera are not missed (Rowcliffe *et al.* 2016).

The density estimate from REM can be thought of as a bias-corrected relative abundance index and, as such, the trapping rate statistic is a key component of the model. This means that many of the sampling design recommendations for relative abundance indices (**Chapter 7-6**) apply equally to studies using REM.

7-8-2 Spatial configuration of sampling points

To satisfy the key assumption of REM – that cameras are placed randomly with respect to animal movement – the simplest solution is to distribute cameras at random, either systematically (to ensure a minimum separation between cameras) or using a simple random design. Although it is practically difficult to achieve complete randomness, **random at the scale of microhabitat** probably suffices. This means cameras should be placed as close to a random point location as possible, but that **small deviations are probably allowable**, assuming the same microhabitat is being sampled.

Deviations of 5-10 m have previously been used as a practical threshold in the field (e.g. Kays *et al.* 2011; Wearn *et al.* 2013; Cusack *et al.* 2015a), but it remains unknown if larger deviations (e.g. > 50 m) might also be allowable. The only study thus far that has tested this, in East African savanna, found marginal differences between the "random" dataset and the dataset in which cameras were placed on game trails up to 50 m from random points, with inferences about carnivore relative abundance particularly affected (Cusack *et al.* 2015a). The effect of using large deviation distances will likely be a function of how heterogeneous the habitat is, with greater deviations from the random points probably more allowable in habitats which are more homogeneous.

This basic recommendation of **random locations can be combined with stratification** as necessary, for example if separate density estimates are required for different habitats or different parts of a broader landscape. This is an effective way of dealing with species, such as the flat-headed cat considered above (**Chapter 7-8-1**), which are highly restricted in their occurrence within a landscape. Strata in which they occur can be defined and sampling can be targeted on those areas, to make better use of limited sampling effort. Stratification can also be a way of dealing with the common problem of inaccessibility in parts of a study area: these areas can be explicitly excluded from sampling, with the final density estimate only applying to those areas which were sampled.

As for relative abundance indices, the recommended inter-trap distance for REM depends on the type of analysis that will be conducted. Most REM studies will simply estimate density over an array of cameras and, in this case, camera traps can be thought of as taking **random point measurements of a continuously-varying density surface** (as for relative abundance indices, above). Dependence among cameras is less of an issue here and short inter-trap distances are therefore allowable in the sampling design. Although it is not currently possible to explicitly **model density as a function of spatially-varying covariates**, such as habitat type, these models are currently in development (under both maximum likelihood and Bayesian frameworks). In this case, each camera becomes a data point in the analysis and should therefore be independent if standard errors associated with model parameters are to be estimated correctly (note that effect sizes will likely remain relatively unbiased). Camera spacing should therefore be larger than the home-range diameters of focal species to ensure independence. In the absence of home-range information, the typical **inter-trap distance of 1-2 km is recommended** to help achieve independence, but models which account for the dependence between camera locations (using random effects) could also be used in theory (this approach has not been demonstrated thus far).

7-8-3 Number of sampling locations

As for relative abundance indices, the recommendation is to sample **at least 20 locations, and ideally more than 50** (Rowcliffe *et al.* 2008). More locations will mean a more precise density estimate. The number of locations required will, however, depend very much on **how patchily-distributed the target species is**: patchily-distributed species will require more sampling locations. More locations will also be needed if cameras are left in place for short periods of time, or if some cameras are separated by only a short distance (e.g. in a clustered design). If multiple strata exist in the sampling design (or covariates on density exist), then each stratum will have to be adequately sampled, multiplying the required sampling effort considerably.

7-8-4 Number of camera trap nights at each sampling point

As for relative abundance indices, a target of **at least 30 trap nights per sampling point** is probably a sensible recommendation for most species. The required number of trap nights will, however, depend on the density of the target species. For a common species, it may actually be more efficient to sample for < 30 trap nights and sample a greater number of locations (if logistics allow). On the other hand, for a species occurring at very low density, > 30 trap nights will likely be required at each location. Greater sampling efforts will also be required if variation in density across space is of interest (e.g. as a function of spatial covariates), to obtain sufficient numbers of counts that are > 1.

7-8-5 Length of study

The trap rate parameter in the random encounter model should be based on **> 10 captures, and ideally > 20**, in order to estimate density with reasonable precision (Rowcliffe *et al.* 2008). As for relative abundance indices, this suggests that minimum total sampling efforts may therefore range between 250 and 20,000 trap nights, depending on animal density (see **Chapter 7-6-5**). For densities typical of many carnivores (and the rarest ungulates), **at least 2,000 trap nights** will be required to obtain 20 captures (Rowcliffe *et al.* 2008).

However, if **other parameters** in the random encounter model, such as activity level and movement speed, are also to be estimated from the camera trap data itself, then **even larger sampling efforts may be required**. Simulations suggest 4-5 times the number of captures (~100) are required in order to estimate animal activity levels and animal speed with reasonable precision (Rowcliffe *et al.* 2016). This means that between **1000 and 10,000 trap nights might be required for most species**, and the rarest members of the community (captured once every 1,000 trap nights) are unlikely to be sampled sufficiently without exceptionally high sampling efforts (> 100,000 trap nights).

There is no formal closure assumption for REM, as for relative abundance indices; the density estimate will be an **average over the period of sampling** (Rowcliffe *et al.* 2008). Having said that, in order to obtain estimates which are both biologically meaningful and useful for management, **shorter time periods are better**. In practice, estimating density over time periods < 1 yr will usually be best, and at finer time-scales still (< 3 months) if changes in threats or management are occurring rapidly. It may be justifiable to **pool data over longer time periods for some of the REM parameters** (e.g. the detection zone parameters), and just alter the trap rate parameter, if sample sizes are insufficient over shorter time periods.

7-9 Occupancy

7-9-1 Assumptions

Occupancy models are closely related to conventional capture-recapture models, and come with some similar assumptions about "closure" and heterogeneity in the data. The basic occupancy model assumes that sampling units are **closed to changes in occupancy** (no local extinctions or colonisations) over the period of sampling. In addition, occupancy models assume that **sampling units** – which could be grid cells or sampling points – are independent. In other words, the detection histories (the sequence of ones and zeroes) for different sites are not related. Occupancy models also assume that **sampling occasions** are independent, i.e. that the detections and non-detections at a site are independent, like repeated flips of a coin. The simplest occupancy models also assume that there is **no heterogeneity** (i.e. no variation) in occupancy or detection probability across sites and across sampling occasions.

As for capture-recapture models, these main assumptions can be relaxed somewhat. This can be done in two main ways. Firstly, you can increase the complexity of the models, by using covariates on occupancy or detection probability to explicitly incorporate heterogeneity into the model. Multi-season (sometimes called "dynamic") occupancy models, which require data over multiple sessions (e.g. different seasons or years), can be used to relax the assumption of closure (MacKenzie *et al.* 2003; Ahumada *et al.* 2013). Secondly, it may be possible to change the interpretation of the occupancy estimate to "**probability of use**" (see below, **Chapter 7-9-5**). This may be an acceptable cost, depending on the objective of the study, in order to relax the assumptions of strict closure.

There is an additional assumption for occupancy models, that **false-positive detections** of species are not made. In general, there is a low risk of violating this assumption in camera-trapping surveys, since photographic records are often unambiguous, especially when compared to other sources of data such as sign surveys. However, surveys should be designed to minimise the risk of any false-positives occurring. In addition, it suggests that a precautionary approach to species identification in images should be used: if an animal cannot be confidently identified to species, then it should not be included as a detection.

7-9-2 Spatial configuration of sampling points

Species occupancy can be estimated from two main sampling designs: 1) **grid-based** designs (sometimes called "plot-based"), and 2) **point-based** designs. Although camera traps actually sample small plots in front of their sensors, the size of these plots is so small that they can be thought of as essentially point-based samples for the purposes of occupancy (Efford & Dawson 2012). Usefully, therefore, camera traps can be used in either grid-based or point-based sampling designs.

Grid-based designs can be made by **overlaying a grid** onto an area of interest and then placing one or more cameras somewhere inside each grid cell (e.g. **Fig. 5-1**) or, if resources do not stretch this far, inside a **random subset of all cells**. The key benefit of this approach is that it allows you to take more creative approaches to increase detection probabilities, which for some species can otherwise be too low to allow occupancy estimation. In particular, it allows you to **target specific microhabitats**, add **additional cameras** to a grid cell (Gálvez *et al.* 2016), or use **other sampling methods**, such as sign surveys or live-traps, in combination with camera traps (Nichols *et al.* 2008).

Point-based designs are, in general, preferred over grid-based designs. This is because the interpretation of occupancy then becomes more straightforward and comparable across studies, as it does not have to be tied to a specific plot size. Specifically, occupancy from point-based designs can be interpreted in terms of the **proportion of area occupied** (PAO) by the species (Efford & Dawson 2012). Point-based sampling designs can be made in a similar way to grid-based designs, but cameras are placed at the **centre of grid cells** (i.e. a systematic random design; **Fig. 7-2**). Technically, cameras should be placed strictly at the grid centre coordinates, but if more flexibility in camera placement is required, so as to increase detection probabilities, cameras can be placed within a certain distance of the grid centres. For example, the TEAM network protocols allow for deviations of 10-20 m from the grid centres (TEAM Network 2011), and up to 50 m may be justifiable in circumstances where accessibility is very poor. However, be aware that this makes the design more similar to a grid-based design and, if the deviations from the grid centres are large, it may mean that occupancy cannot confidently be interpreted in terms of PAO.

The separation between grid lines, or between sampling points, should be at least **one home-range** diameter for the target species. This has two effects. Firstly, separation by at least one home-range diameter reduces the chances that the same animal is captured in neighbouring cameras within a short period of time, which might cause dependence between detection histories. This remains a poorly-explored facet of camera trap data, and cameras spaced apart by less than one home-range diameter may still show statistical independence (see **Box 7-1**). For occupancy detection histories, we are only aware of one exploration of this issue: camera traps within a single home-range of the guiña (*Leopardus guigna*) generally yielded dissimilar detection histories, but that there was some evidence of increased similarity for cameras < 300 m apart (Gálvez *et al.* 2016). It is also theoretically possible to account for non-independence by incorporating random effects into occupancy models, but this approach has been poorly explored to date and is not currently implemented in standard software (see Rota *et al.* 2016b).

The second reason for separating cameras by at least one home-range is because this has implications for the **interpretation of the occupancy estimate** (as noted in **Chapter 6-5**). If there is more than one occupancy site (grid cell or point location) per home-range, then occupancy becomes related both to the habitat-use of individual animals and the broader-scale distribution of the species. It also means that the strict closure assumption is violated, since animals may be unavailable for capture during a given sampling occasion. As a result, if cameras are separated by less than one home-range, an interpretation of the occupancy estimate as "**probability of use**" is preferred over "probability of occupancy" (Mackenzie & Royle 2005). Note that simulations suggest a more conservative rule that occupancy grid cells should be more than ten times the home-range size of a species (Efford & Dawson 2012). Although this recommendation may be difficult to achieve in practice for species with very large home-ranges, such as large carnivores, it may be achievable for species with smaller home-ranges.

Guidelines for the Wildlife Picture Index (WPI) and the TEAM network recommend 2 km spacing of camera traps, although 1-4 km is also permissible (O'Brien 2010; TEAM Network 2011). In a review of species studied using camera traps, the median home-range size across species was 4.8 km^2 (Burton *et al.* 2015), which would require ~2.2 km spacing. We recommend that **spacing is tied to the home-range sizes of target species**. In the absence of home-range information, we recommend at least 1 km spacing, but note that shorter distances may be allowable for species with relatively small home-ranges. For broad-spectrum occupancy surveys of multiple species, spacing should be based on the species with the largest home-range sizes (otherwise you will need to refer to estimates for these species as "probability of use").

7-9-3 Number of sampling locations

The number of occupancy sites (grid cells or point locations) to include in your sampling design depends on how patchy the occurrence of the species is. For common species, with an occupancy greater than 0.8, occupancy can be estimated reasonably precisely with ≤ 30 sites, irrespective of whether the species is easily detectable or not (Shannon *et al.* 2014). However, for many species, 30-60 sites can be required for reasonably precise occupancy estimates, with more sites needed for less common species (Shannon *et al.* 2014). Note, these recommendations are for the simplest occupancy models; **more sites will be needed if covariates** on occupancy or detection probability are to be added into models (as will most often be the case).

For very rare species, with an occupancy of less than 0.1, then a large number of sites (100+) will likely be required to have any chance of producing an occupancy estimate (O'Brien 2010). The difficulties with estimating occupancy for very rare species are compounded by the fact that there is often a positive correlation between occupancy and detectability (e.g. Shannon *et al.* 2014), meaning that many rare species also have low detection probabilities. When this is the case, for example if detection probability is < 0.05, it may be very difficult to obtain any occupancy estimate at all (O'Brien 2010; Shannon *et al.* 2014), or it may erroneously be estimated as 1 (a "boundary effect"; Guillera-Arroita *et al.* 2010). When this is the case, another option is to employ hierarchical multi-species occupancy models, in which occupancy and detection probability parameters for rare species are estimated by "borrowing strength" from information on more common species (e.g. Tobler *et al.* 2015; Wearn *et al.* 2017).

Camera-trapping guidelines for the WPI and TEAM network recommend 100 and 60-90 sampling locations, respectively (O'Brien 2010; TEAM Network 2011). As a general recommendation, we suggest **a minimum of 40 sampling locations** for occupancy surveys, but with the recognition that **100+ sampling locations may be required** if covariates are to be included, or if the target species is relatively rare.

7-9-4 Number of camera trap nights at each sampling point

The number of repeat samples that are required to be taken at each site crucially depends on how detectable the species is. This aspect of survey design, more than any other, has been relatively well explored using simulations and empirical data (Mackenzie & Royle 2005; Bailey *et al.* 2007; Guillera-Arroita & Lahoz-Monfort 2012; Shannon *et al.* 2014; Gálvez *et al.* 2016). Broadly, **the less detectable a species is, the more repeat samples** that are needed. Although just two days of trapping are needed to fit an occupancy model in theory, much higher numbers of samples are needed in practice. Helpfully, camera traps are a highly efficient method for obtaining repeat samples, since they sample for multiple days at no additional cost.

If detection probabilities are very high (> 0.5), less than one week of sampling may be sufficient (Mackenzie & Royle 2005; Guillera-Arroita *et al.* 2010), but detectability is rarely so high in camera trap surveys. Simulations suggest that for detection probabilities typical of most species in camera trap surveys (< 0.2), a minimum of 2 weeks sampling will be required, and more likely **> 30 days for a reasonably precise occupancy estimate** (Mackenzie & Royle 2005; Guillera-Arroita *et al.* 2010; Shannon *et al.* 2014). Both the WPI and TEAM network protocols use 30 days of sampling at each site (O'Brien 2010; TEAM Network 2011)

For species which are especially elusive and difficult to detect (with detection probabilities < 0.05), **80-100 days of sampling may be required** (Shannon *et al.* 2014). This intensity of sampling would be almost impossible to achieve with sampling methods requiring human observers (e.g. bird point counts), but is a realistic proposition for camera-trapping. Under a grid-based survey design, multiple cameras can also be added to each site to increase the number of occasions. Once the transport costs of doing surveys are considered, the deployment of multiple cameras in clusters can be a more efficient way of sampling, compared to leaving single cameras out for a long period of time (Gálvez *et al.* 2016). It is also possible to increase detection probabilities by **pooling detections across multiple camera trap nights**, so that each sampling occasion is, for example, five trap nights (a similar suggestion was made above, for capture-recapture studies; **Chapter 7-7-4**). This can also help to satisfy the assumption of independent sampling occasions, and can improve the fit of models (Tobler *et al.* 2015).

As for other study types above, there is usually a **trade-off** to be made in occupancy studies, between sampling more sites or sampling fewer sites for more trap nights (**Table 7-1**). In general, if a species is relatively common (high occupancy), it is most efficient to sample fewer sites for a longer period (Mackenzie & Royle 2005; Shannon *et al.* 2014; **Table 7-1**). The same approach is best if a species is very poorly detectable. If a species is rare and patchy in its distribution (low occupancy), then all else being equal it is generally better to move cameras more frequently, sampling more sites for a shorter period of time (Mackenzie & Royle 2005; Shannon *et al.* 2014; **Table 7-1**). Pilot studies and simulations can help to inform the best compromise for the aims of a particular study.

		Detection probability		
		Low	Medium	High
Occupancy	High	↓ Sites ↑ Days	↓ Sites ↔ Days	↓ Sites ↓ Days
	Medium	↑ Sites ↑ Days	↔ Sites ↔ Days	↔ Sites ↓ Days
	Low	↑ Sites ↑ Days	↔ Sites ↑ Days	↔ Sites ↔ Days

Table 7-1. Tradeoffs in sampling design for occupancy studies using camera traps, after Shannon *et al.* (2014). Symbols indicate high (↑), intermediate (↔) and low (↓) levels of effort in each case.

7-9-5 Length of study

Given that 40 or more sites, each sampled for 30 or more trap nights, will be the minimum requirement for most occupancy studies, this suggests that at least 1,200 trap nights will be needed. Greater sampling efforts will be required if covariates are to be included in modelling. For rare and poorly detectable species, sampling efforts of **at least 5,000 trap nights** will be needed (Shannon *et al.* 2014). These recommendations are similar to those for a capture-recapture study (**Chapter 7-7-5**).

Sampling should be done in the **minimum time possible**, in order to help satisfy the assumption that sites are closed to changes in occupancy. There are no hard-and-fast rules for what period of time is too long, as temporal changes in occupancy have been poorly studied. As noted above (**Chapter 7-5-5**), there is evidence that site closure can be violated over as period as short as 1-3 weeks for birds sampled using point counts (Rota *et al.* 2009). However, camera trap studies primarily target medium- and large-sized birds and mammals, likely with slower life histories than these species. In the absence of empirical data, we suggest that an assumption of a **3-6 month period** of site closure seems reasonable for these species. An alternative recommendation is to make sure that sampling is done within a single season (e.g. TEAM Network 2011). At higher latitudes, in particular, occupancy will likely vary dramatically depending on the season.

As for capture-recapture models, the **closure assumption can be relaxed** if you can assume that any changes are occurring at random (Kendall 1999; MacKenzie *et al.* 2004). In the case of occupancy models, the assumption would be that there is no directional change in site occupancy (MacKenzie *et al.* 2004), as might occur if animals permanently emigrate from sites during sampling. However, this relaxation of the closure assumption comes at the cost of a fundamental change in the interpretation of the final occupancy estimate, from "probability of occupancy" to "probability of use" (e.g. Burton *et al.* 2012; Tobler *et al.* 2015).

7-10 Behaviour

Behavioural studies vary greatly in their aims, and the ecological parameters that are therefore of interest. Behaviours as disparate as predation, foraging, mating, or parental care might be of interest. Some studies might be primarily qualitative, whereas others might be more quantitative. The focus of the study could be on a particular location (such as a lekking site or a fruiting tree) or on a particular species. However, as for the study types we have considered above, the starting point is to establish what the **key assumptions** of the modelling are, and then design the sampling appropriately with this in mind.

For example, imagine you are interested in the rate at which a given behaviour occurs in a species (e.g. vigilance: Schuttler *et al.* 2017), and how this differs across major habitat types in your study area. If your aim was to make inferences about the population in your study area as a whole, then you would want to take a representative sample of individuals, and you would want to observe them at random locations and random times of the day. All of this could be achieved using random sampling points, stratified by habitat type, with camera traps set to trigger throughout the 24 hr period. Cameras would ideally be sufficiently spaced apart to obtain samples from lots of different individuals (e.g. 1 km apart, depending on the species). Similarly, the number of sampling points, and how long each is sampled for, would have to be sufficient in order to obtain a reasonable number of behavioural observations in each habitat type (> 20 per stratum would be a sensible minimum target). The length of the study would ideally not be too long, for example restricted to a single season, so as to provide a snapshot of the prevalence of the behaviour in different habitat types in the absence of any temporal trends in the behaviour (temporal or seasonal trends could be a focus of follow-up surveys).

This basic approach to sampling design for a behavioural study would be suitable for the study of **activity patterns**, which is a common use of camera traps. In this case, some aspects of sample size have been investigated (Ridout & Linkie 2009; Rowcliffe *et al.* 2014). This work suggests that a sample size of **20-25 observations** will offer useful insights into activity patterns over a 24 hr period, but that larger samples (> 100) will be needed to characterise the activity patterns with any reasonable level of precision, especially if the pattern has a complicated shape (Ridout & Linkie 2009; Rowcliffe *et al.* 2014).

7-11 Monitoring of people or their activities

An increasing number of researchers and conservationists are using camera traps to shine a light on which areas of a landscape are being used by people, how intensely different areas are being used, and what people are doing there. In many ways, these are very similar questions to those we might want to ask about animal populations, and a lot of the same survey design recommendations apply (see previous Chapters). However, care must be taken to ensure that modelling assumptions are being met. The major difference between animal and human populations will often be that human populations are **temporary migrants** (e.g. on a day-to-day basis), rather than permanent residents in a study area, and that their **habitat-use is highly restricted** (primarily using available trails). People will also often **react to camera traps** when they see them, and may alter their movements and behaviour as a result. This may be particularly important when monitoring illegal activities, which will be under-estimated if people learn to avoid or sabotage cameras.

Camera traps are increasingly being used in anti-poaching activities and, in such cases, the spatial layout of cameras will usually be highly specific to a given scenario. For example, they may be used to fill gaps in the knowledge of park rangers, by monitoring sites which rangers cannot effectively patrol themselves (e.g. Hossain *et al.* 2016). Alternatively, they may be used to monitor specific **hotspots of poaching activity**, such as places where animals targeted by poachers habitually congregate (e.g. swampy clearings for forest elephants). If sufficient cameras are available, they can also be used to erect a “**virtual fence**” around the perimeter of a particular site. The application of camera traps for anti-poaching is relatively new, and the effectiveness of different survey designs remains poorly explored.

	Survey design recommendations						
Type of camera-trapping study	**Placement strategy for cameras**	**Sampling point spacing**	**Number of sampling points**	**Number of trap nights per point**	**Total sampling effort**	**Survey duration**	**Key references**
Qualitative recommendation	*As randomised as possible*	*As large as possible (except for capture-recapture)*	*As many as possible*	*As many as possible*	*As large as possible*	*As short as possible*	Any textbook on ecological field techniques
Rapid inventory	Targeted placement; random placement if target species poorly known	No minimum	No minimum, ideally ≥ 20	No minimum, but ideally ≥ 30; < 30 sufficient for highly detectable species	No minimum, ideally > 1,000 trap nights	No maximum	Targeted: Tobler *et al*. (2008); Random: Wearn *et al*. (2013)
Diversity	Random placement	Ideally ≥ 1 km, but closer spacing may be justified	Minimum of 20, ideally ≥ 50	Ideally ≥ 30 to cover all species	Ideally > 1,000 trap nights	Ideally < 6 months	Tobler *et al*. (2008); Cusack *et al*. 2015a)
Relative abundance	Random placement	No minimum, but ideally ≥ 1 km	Minimum of 20, ideally ≥ 50	No minimum, but ideally ≥ 30	Ideally > 2,000 trap nights	No maximum, but ideally < 12 months	Rowcliffe *et al*. (2008); Wearn *et al*. (2013); Cusack *et al*. (2015a)
Capture-recapture	Targeted placement	Suitable spacing depends on home-range of target species; 1-4 km is typical	Minimum of 20, ideally ≥ 40	≥ 30 required for all but the most detectable species; 60-120 if detectability is low	> 1,000 trap nights for most species; > 3,500 if detection probability is low	Depends on target species; ideally < 3 months	Sollmann *et al*. (2012); Tobler & Powell (2013)
Random encounter modelling	Random placement	No minimum, but ideally ≥ 1 km	Minimum of 20, ideally ≥ 50	No minimum, but ideally ≥ 30	Ideally > 2,000 trap nights; 2,000-10,000 if animal activity and speed to be estimated	No maximum, but ideally < 12 months	Rowcliffe *et al*. (2008); Rowcliffe *et al*. (2016)
Occupancy	Random or targeted placement	Minimum spacing should be larger than home-range of target species; ≥ 1 km is typical	Minimum of 40, ideally ≥ 100	≥ 30 required for all but the most detectable species; 80-100 if detectability is low	> 1,000 trap nights required for majority of species; > 5,000 trap nights for rare and poorly detectable species	Depends on target species; ideally < 6 months	Mackenzie & Royle (2005); Guillera-Arroita *et al*. (2010); O'Brien (2010); Shannon *et al*. (2014)
Behaviour	Usually targeted placement	Dependent on study aims					
Monitoring of people or their activities (e.g. anti-poaching)	Random or targeted placement depending on study aims	Dependent on study aims					

Table 7-2. Recommended survey design characteristics for the major types of camera trap study, as taken from a broad review of the camera trap literature. Key references provide survey design advice or draw attention to important survey design considerations. The quantitative recommendations made here will often need to be adjusted to the specific context of a single study; this process can be informed by pilot studies or simulation work.

Camera traps vary in their specifications. Choosing an appropriate model to suit your study's objectives, target species and environment could mean the difference between success and failure.

Image: © Oliver Wearn

8 WHAT CAMERA TRAP TO CHOOSE

HIGHLIGHTS

- Camera traps vary a lot in their specifications, and this can have important consequences for how well they perform for a given study aim, on a given type of animal, in a given context
- Given the rapid pace at which new camera trap models are released, it is not possible to recommend specific camera trap models
- The best approach to identifying what camera trap to choose is to identify the broad type of camera that you require, and then the specific features required in order to achieve your study's specific aims
- Most research and monitoring purposes call for a mid- to high-end camera trap, equipped with an infrared flash, large detection zone and fast trigger speed
- Important exceptions to this broad recommendation include: a white flash (in most cases) for capture-recapture studies, and a video or "near-video" mode for studies intending to use random encounter modelling
- For camera-trapping small mammals or small birds, a high-end camera trap with a good infrared sensor and fast trigger speed is required; white flash should be considered to aid species identifications
- For arboreal camera-trapping, required camera trap features include a large detection zone, fast trigger and recovery speeds, and wide field of view
- Ectothermic species remain a challenge for the majority of commercial camera traps and must be combined with specific methods (e.g. deployment at certain times of day, or using time-lapse) in order to help overcome this; a setup with a direct trigger (e.g. active infrared sensor or pressure pad) may be more effective
- Environments with high rainfall, snowfall or humidity will be problematic for most commercial camera traps; a high-end camera trap with good protection against the elements is recommended (e.g. a fully-sealed casing and conformal coating on the circuit board)
- In hot environments, passive infrared sensors may fail to detect a difference between the surface temperature of target animals and the background; a camera setup with a direct trigger may be more effective
- In open environments, and when camera-trapping in trees, a high-end camera trap which is less prone to misfires from moving vegetation will be beneficial (although all camera traps are susceptible to this problem); it may also be helpful to use cameras which allow the sensitivity of the infrared sensor to be reduced
- For camera-trapping in areas which come with a high risk of theft, consider the security options that are compatible with a given camera trap model (e.g. cable locks and security cases)
- You should buy as many camera traps as you can, but certainly at least as many as your study demands in order to be robust and useful; you can estimate the minimum number of cameras you'll need based on your sampling design and information about how long it will take to install, move and collect cameras in the field
- Published studies comparing camera trap models often become quickly out-of-date; a better option is to reach out to the camera-trapping community to gauge opinions about a specific camera trap model for a given task

The rapid growth of the commercial camera trap market, driven mainly by recreational hunters in North America and increasingly by wildlife hobbyists, has led to a confusing array of different manufacturers and models. For experienced and novice camera-trappers alike, it can be difficult to sort out which of the many features listed by manufacturers and sellers are actually important. Whilst we do not make recommendations about specific camera trap models here – because they would quickly be out of date – we do provide some recommendations on how to go about deciding what camera trap to buy (and how many), and the features you should look for given your aims.

8-1 What broad type of camera trap do you require?

As outlined in **Chapter 4**, camera traps cluster into just a few broad types (**Table 4-3)**, and this can help to slim down the choices. If you are aiming to formally estimate one or more state variables, then in the majority of cases, a mid- to high-end camera trap is required. These employ tried-and-tested technology, such as a passive infrared sensor and infrared flash. It is best to avoid the temptation to purchase budget camera traps for robust monitoring. Although some budget models ostensibly offer many of the same features as mid- and high-end models, they will be far less reliable and will likely not turn out to be cost-effective (e.g. Newey *et al.* 2015). For community engagement and educational purposes, or for doing informal inventory work, there is perhaps more flexibility on the type of camera trap that will be suitable, and a budget camera trap might suffice. For very specific or unusual use-cases, such as behavioural monitoring or herpetological surveys, it is difficult to make general recommendations about what kind of camera trap to choose. In this case, a custom-made camera trap, or an "experimental" type of camera trap, might be required. A sound knowledge of how camera traps work (**Chapter 4**), and what options are available (**Table 4-2**), will guide your purchasing decisions.

8-2 What specific camera features are required?

Once you have decided on the broad type of camera trap that will be suitable, then you should think about any specific camera features that will be required in order to achieve your aims. If your camera trap study fits neatly into one of the eight types outlined in **Chapter 7** (**Fig. 7-1**), then it is possible to be quite precise about some of the features that will be needed (**Table 8-1**).

For **rapid inventory work**, the aim is simply to detect as many species as possible, as quickly as possible. Given that no formal modelling assumptions need to be met in this case (**Chapter 7-4-1**), a white flash camera is likely the best option, as it will offer the best chance of identifying a wide range of species, including small mammals and other species which are "cryptic" under infrared flash. Although white flashes may lead to "trap-shy" behavioural responses and, for Xenon flashes in particular, slow recovery times, this is not a problem for rapid inventory studies per se. A camera trap with a large detection distance and wide detection angle is also important, to maximise the area sampled. Video camera traps can also be considered for rapid inventory work, for documenting the behaviour of very poorly known animals and generating engaging outreach material. However, this has to be weighed against the slower trigger times that are typical of video modes, and the chances that some species may be missed altogether as a result.

Studies of **diversity and occupancy**, although involving different assumptions, call for similar features in a camera trap. The aim for diversity studies is to detect as many species as possible, ideally by sampling individuals at random. For occupancy studies, the aim is to make the probability of making detections of a species as high as possible and to not introduce too much heterogeneity in detection probabilities. In both cases, therefore, it's important to make as many detections as possible, whilst not disturbing animals in the process. This calls for an infrared flash, large detection distance, wide detection angle and fast trigger speed.

For assessing abundance, whether using a **relative abundance index** or **random encounter modelling**, the aim is to make as many detections as possible, and to accurately count the number of individuals passing in front of the camera. Note that for inventory work, as well as diversity and occupancy studies, the number of individuals was not strictly required. To make accurate counts, a fast trigger and recovery speed is necessary, ideally with a "near-video" mode. A large detection distance and wide detection angle will also be useful for maximising the number of detections made. An infrared flash is required, since neither analysis methods can account for any behavioural effects of white flash. For random encounter modelling, there is the additional consideration that the near-video sequences will be used for **animal tracking**, in order to estimate movement speeds. It is recommended that trigger speeds must be < 1 s, and near-video recorded faster than 1 frame per second, so that faster movements are not under-sampled (Rowcliffe *et al.* 2016). In addition, only movement sequences which show undisturbed behaviour should be used to estimate speeds, so it can be useful to use a "no-glow" black flash to reduce instances of animals reacting to cameras.

The demands for a **capture-recapture** survey are perhaps most distinct from the other types of study. In this case, the aim is to not only make as many detections as possible of the target species, but also make sure that animals in the images are individually-identifiable. In the overwhelming majority of cases, this demands a white flash camera trap and, ideally, Xenon white flash, which is less likely to produce images with motion blur. Xenon white flash delivers a strong and instantaneous (about one thousandth of a second) white light source, producing crisp and well-exposed colour images of pelage patterns or other characteristics used for identification. Although white LED flash may carry a greater risk of motion blurring, the quick recovery times possible with this kind of flash may mean that more images can be captured of individuals, making identification possible anyway. A large detection distance, wide detection angle and fast trigger speed are also useful for making sure detection probabilities are high. Fast recovery times are less important for this kind of study, since most individually-identifiable animals are solitary (e.g. striped and spotted cats), so there is less danger of missing trailing individuals. Although some individuals may have dependent young that could be missed with Xenon flash cameras with slow recovery times, these are not typically counted in capture-recapture estimates. If accurate counting of group size is important for the study, this could be another reason to use white LED flash. Note that it is often possible to identify individuals using infrared flash, but more detections will inevitably have to be thrown away, reducing detection probabilities. For a highly-detectable species, the benefits of using infrared flash for other study aims (e.g. random encounter modelling of other species) may outweigh the cost of reduced precision in the capture-recapture estimate.

Behavioural studies are hugely variable, and may involve monitoring of focal resources (such as fruiting trees, water holes or mineral licks) or focal species (e.g. animals on their nest or at their breeding ground). You should think carefully about any ecological parameters you are aiming to estimate (e.g. a visitation rate, a provisioning rate or the timing of phenological events), and the assumptions that are embedded within them. This will guide your decisions about what camera trap features are desirable and permissible. In most cases, an infrared flash (and ideally black flash) will be required to observe undisturbed behaviours, as well as a fast trigger speed so that fleeting behaviours are not missed. Video may be necessary to collect high-resolution data on subtle behaviours (such as direct interactions between individuals or food handling behaviours). Time-lapse may be a more reliable and standardised method of monitoring behaviour in some cases (e.g. arrival of individuals at their breeding grounds), especially if the field of view being monitored is vastly greater than the detection zone. Also consider if you require a non-standard lens, such as a telephoto (useful for monitoring behaviour at a distance), macro (for monitoring behaviour at close range, such as a nest or feeding station) or wide-angle (for monitoring a large field-of-view). Finally, some of the more expensive camera traps allow for on and off times to be scheduled, which may be useful to save battery life if the behaviours of interest only occur at specific times of day.

For studies which specifically target **people**, the aim is usually to make observations without the camera being detected. This is especially the case if an area is being monitored for illegal activities, such as poaching, and the camera may be at risk of theft or vandalism if discovered. Camera traps should therefore be as covert as possible. Since vision is the dominant sense in humans, small and camouflaged cameras will work well, combined with unusual deployment heights (e.g. in trees above head height, and angled downwards). Camera traps should also have an infrared flash, either "low glow" (which can be visible to humans from certain angles) or "no-glow". A fast trigger speed is also essential, since people often walk relatively fast compared to most other terrestrial animals.

For **anti-poaching** purposes, a camera with a rapid recovery time, ideally with "near-video" capabilities, will also be essential for collecting as much evidence as possible and for identifying individuals in the images. Wi-Fi camera traps, which are able to send images to a central base station in a secure place nearby, will mean that data is not lost if any cameras are stolen or destroyed. However, camera traps will be most effective for anti-poaching if they can provide "real-time" data to rangers. In this way, they can be used to prevent poaching, rather than just providing evidence after poaching has already happened. For this, cellular cameras will often be required, with a sufficiently long battery life (or external power source) so that they do not require too much time investment by rangers. Cellular cameras can be programmed to send images to mobile phones in the field, as well as to a central operations hub, such as a ranger station. However, it is important to have realistic expectations of current cellular cameras (see **Chapter 4-2-3**) and, ideally, carry out pilot study work before deciding that they are a viable option.

Study type	Key camera trap considerations	Justification
Rapid inventory	Xenon or LED white flash; large detection zone; consider video	Best chances of identifying as many species as possible and covering a large sampling area
Diversity	Infrared flash; fast trigger speed; large detection zone	Detecting as many species as possible with minimal disturbance
Relative abundance	Infrared flash; fast trigger and recovery speed; large detection zone; multiple images per trigger; “near-video” mode	Making as many detections as possible with minimal disturbance, and allowing for more accurate estimates of group size
Capture-recapture	Xenon white flash; consider white LED flash; fast trigger speed; large detection zone;	Prioritising the identification of as many individuals as possible
Random encounter modelling	Infrared flash; consider “no-glow” infrared flash; fast trigger and recovery speed; large detection zone; multiple images per trigger; “near-video” mode	Allowing the number of animal-camera “contacts” to be accurately estimated, including for group-living animals, and allowing for movement speeds to be estimated
Occupancy	Infrared flash; fast trigger speed; large detection zone	Making as many detections as possible with minimal disturbance
Behaviour	Infrared flash; consider “no-glow” infrared flash; video mode; fast trigger and recovery speed; consider “near-video” mode; consider time-lapse; consider non-standard lenses (telephoto, macro or wide-angle); consider if programmable schedule is needed	Recording in detail as much animal behaviour as possible with little or no disturbance
Monitoring of people or their activities (e.g. anti-poaching)	Infrared flash; fast trigger and recovery speed; multiple images per trigger; “near-video” mode; consider feasibility of wireless or cellular; long battery life or external power; small size; camouflaged; consider video	Making as many detections of people as possible without giving away the presence of a camera, and possibly sending data either to a base-station (for secure storage) or to relevant authorities (to immediately act upon)

Table 8-1. Camera trap features that are desirable for each of the major types of camera trap study.

8-3 Additional considerations

8-3-1 Study taxa

If you are studying a **medium-to-large mammal**, then you are in luck. Commercial camera traps are designed primarily for game species such as deer, and the detection circuitry that is best for a deer will also work well for many other mammal species. If, however, your species is smaller, faster, or not as warm as a deer, then you may need to think more carefully about the camera features you'll need.

Small mammals, conventionally all those mammals < 1 kg, are often left out of camera-trapping studies, or simply lumped together into broad categories such as "rat" or "squirrel". In part, this is because older camera trap models did not consistently detect species < 1 kg. The best passive infrared sensors on the market today, however, can reliably detect small mammals < 100 g, provided they are **within 2 m of the sensor** (Rowcliffe *et al.* 2011). Small mammals at this range can quickly leave the field of view, so a fast trigger time is also an important camera feature. Small mammal detections are also often neglected because of the difficulty of identifying many small mammal species under infrared light, due to their similar sizes and overall morphologies. White flash can be used to overcome this in many circumstances, allowing species to be identified on the basis of their pelage colouration.

For camera-trapping **arboreal mammals**, an excellent sensor is critical, since detection zones in the canopy might be restricted to just a single branch in front of the camera. In addition, animals in the canopy can easily leave the field of view both horizontally and vertically, and are typically fast-moving, meaning that they might only be visible for a short period of time. As a result, a fast trigger, rapid recovery time, "near-video" mode, and wide field of view, will all maximise the chances of successful species identification in the canopy. A wide field of view will also allow for more accurate counting of group size in the three-dimensional environment of the canopy.

Relatively few studies have investigated how effective camera traps are for surveying **birds** (O'Brien & Kinnaird 2008; Thornton *et al.* 2012). However, large terrestrial birds (e.g. pheasants) present a temperature contrast as large as similar-sized mammal species (Meek *et al.* 2012), and camera traps are likely a highly effective method for surveying such species (Thornton *et al.* 2012). For smaller bird species (< 100 g), a higher-end camera trap with good detection circuitry should be able to detect individuals, provided they are **within 2 m of the sensor**. As for small mammals, birds at this range can quickly leave the field of view, so a fast trigger time is essential. Feather colouration is critical for identifying many species of bird, meaning that the black-and-white images provided under infrared flash can be problematic. Although most birds are diurnal, intensely shaded environments (e.g. tropical rainforests) may not provide enough natural light for a camera trap, in which case white flash should be considered to aid identifications. For dedicated bird surveys, a feeder or other baiting method may be an effective option. In this case, a camera trap with a macro lens will be the best option, allowing the camera trap to be mounted close to the feeder for easier identification.

Passive infrared sensors, typically of commercial camera traps, are good for warm-blooded animals which are a different surface temperature to their background environment (see **Chapter 4-1-1** and **Box 4-1**). **Ectothermic species** do not typically show this temperature difference, and so a camera setup with a **direct trigger** may be more effective. A few studies have successfully demonstrated this (Alexy *et al.* 2003; Leeb *et al.* 2013), although direct triggers are not currently available for the majority of commercial camera traps. It may still be possible to use an "off-the-shelf" camera trap with passive infrared sensor if the target species shows a temperature difference in certain locations (e.g. basking spots) or at certain times of day (e.g. around the hottest part of the day). It is also possible to exploit passive infrared sensors by enhancing the temperature contrast between an ectothermic species and the background scene with an artificial substrate, such as a cork tile

(Welbourne 2013). Finally, it may be worth instead considering using camera traps with a time-lapse setting, which allows for images to simply be taken at regular intervals, with no input from a trigger. This comes at the cost of much greater numbers of blank images and a much-reduced battery life, but may be a satisfactory solution for monitoring ectotherms in certain circumstances (e.g. Chowfin & Leslie 2014).

These recommendations for specific taxa (**Table 8-2**) may conflict with those recommendations given above for a given study type (**Table 8-1**). However, with careful study design and appropriate analyses, it may be possible to accommodate these required features without violating the assumptions of the chosen modelling approach. Where this cannot be assured, then a decision must be made whether the **risks of introducing potential biases** are acceptable or not. For example, white flash images are particularly useful for distinguishing species of small mammal by pelage colouration, which might otherwise look similar in their morphology. For occupancy, white flash is not generally recommended, as it may introduce additional heterogeneity in detection probabilities, if for example some individuals become trap-shy. In this case, a decision must be made whether the risks of introducing some amount of bias is outweighed by the benefits obtained from separately estimating occupancy for each cryptic species.

Taxa	Camera trap considerations	Methodological considerations
Individually-identifiable species (e.g. spotted or striped animals)	Xenon white flash; fast trigger speed	Paired cameras; consider the use of baits or lures
Medium and large mammals	Infrared flash; fast trigger speed; multiple images per trigger; “near-video” mode	
Small mammals	Xenon or LED white flash (for colour); fast trigger speed; large detection zone (i.e. excellent detection capabilities); consider active infrared sensor	Mount cameras close (< 2 m) to the targeted detection area; consider vertical mounting (e.g. with a tripod) and baiting (e.g. with a bait canister)
Arboreal mammals	Infrared flash; fast trigger speed; multiple images per trigger; “near-video” mode; wide field of view	Ball-head mounting, which is screwed or strapped to a tree branch; consider setting the sensitivity of the infrared sensor to low, to minimise misfires
Birds	Infrared flash; fast trigger speed; large detection zone	For small species of bird, mount cameras close (< 2 m) to the targeted detection area
Ectothermic animals (e.g. reptiles)	Direct trigger (active infrared sensor or pressure sensor); consider if passive infrared sensor or time-lapse are viable	If using passive infrared, consider using a drift fence (as used for pitfall sampling), vertical camera mount (e.g. with a tripod) and a cork tile background; alternatively, focus on locations or times of day in which species are a different temperature to their backgrounds

Table 8-2. Camera trap features that are desirable for studying various types of animal, as well as methodological aspects to consider.

8-3-1 Deployment environment

Extreme environments and electronics do not combine happily. If you are deploying camera traps in an extreme environment, you should consider some additional aspects of camera trap design when choosing which model to use.

In environments with **high precipitation** (rain or snow), a waterproof case is essential. Ideally, this should have an O-ring and firm latch closure design to properly seal the case. Even very small gaps in the case, such as around the camera lens window or battery cover, can allow water to seep in over a period of weeks, potentially damaging the electronics beyond repair. **Humid environments** present a slightly different challenge, but can equally damage camera traps over long deployments of several weeks. Humidity can rust electronics, including the circuit board and the connections for the batteries. Look for cameras with a “conformal” coating on the circuit board to help combat this problem (e.g. the Reconyx Professional series of cameras). Conformal coatings can also help in coastal and marine environments, to combat corrosion by salt.

In **hot environments**, such as open desert or grassland environments in the tropics, passive infrared sensors may cease to be useful in detecting warm-blooded animals. Passive infrared sensors work by detecting a temperature differential between the surface of the environment and an animal, with the differential ideally being greater than ~3 °C (Meek *et al.* 2012). In hot environments, the background environment may be a similar temperature to the body surface of a warm-blooded animal, making detection unreliable. Whilst the core body temperatures of warm-blooded animals are relatively well known, often ranging between 34 and 42 °C (Meek *et al.* 2012), their surface temperatures under different conditions remain poorly known (Cilulko *et al.* 2013). As a result, it is difficult to make a general prediction about when passive infrared sensors will fail, although it is safe to assume that it remains an undiagnosed problem in many studies. In such cases, an alternative sensor may be needed, such as an active infrared, pressure or microwave sensor. It may also be possible to restrict inferences to a period of the 24 hr cycle in which passive infrared sensors work more effectively (e.g. at night in deserts), or to explicitly account for time-varying detection probability during modelling of the data.

In **open environments** with lots of vegetation at ground level, or in **arboreal camera-trapping**, a large number of misfires can be generated by vegetation which is heated by the sun. This can be a significant drain on battery life and memory capacity, not to mention the time it takes to review the data. Modifications to the sampling design, and careful camera setup, can help with this problem (e.g. only deploying cameras in shady microhabitats). However, it helps to have a high-end camera trap with detection circuitry which is more robust to this problem (some budget camera trap models are particularly prone to misfires). Alternatively, it can help to have a camera trap which allows the user to adjust the sensitivity of the passive infrared sensor. By lowering the sensitivity of the sensor, fewer misfires will result, but it is important to remember that this may come at the cost of fewer animal detections as well (effectively, it lowers the detection probability). Many camera trap models can be programmed to operate only during certain times of the day; this can be used to sample at night only, when misfires from heated vegetation should be less of a problem.

In environments with a particularly **high risk of theft**, especially **urban** and **agricultural habitats**, it is also important to consider the security options for a given camera trap model. Some camera traps have an external case which is compatible with a cable lock, allowing them to be quickly locked to an immoveable object. This can be useful as a minimal security option in some circumstances, primarily acting as a deterrent to opportunistic theft. This option potentially leaves the batteries and memory cards at risk of theft, but many mid- and high-end camera traps can be locked closed using a padlock. For higher levels of security, reinforced steel enclosures are available for some camera trap models, produced either by the manufacturer themselves (e.g. Bushnell or Reconyx) or by third-parties (e.g. Custom1 Enterprises). These can be secured to immoveable objects using cable locks or lag bolts, and offer better protection against theft and vandalism, albeit at the cost of increased conspicuousness and increased bulk during transport. It may also be possible to have a custom security enclosure made locally if one is not commercially available (e.g. **Fig. 10-8**), albeit potentially at a higher cost. Finally, some camera traps can be locked using a PIN code, much like mobile phones. This renders them useless to thieves, but only acts as a theft deterrent if the thieves are aware of this feature.

8-4 How many camera traps to buy

The first question that is often asked when planning a camera trap study is "how many camera traps do I need to buy?" In many ways this is the wrong question to be asking: the answer is always "as many as you can beg, borrow or steal!" A better question in most cases is "**what is the minimum number of camera traps** I need to achieve my objects?" Similarly, another good question is "can I achieve my objectives with the number of camera traps that I can afford?" If the answer is "yes", then the study will likely be a successful and wise investment of conservation funds, but if the answer is "no", the temptation to just press on anyway with a "hope for the best" attitude is best avoided.

So how do you work out what the minimum number of camera traps you'll need is? The starting point is your ideal sampling design (see **Chapter 7**), and in particular the **number of sampling points** you'll need to cover and **how long** each of them needs to be sampled for. The second consideration is **how much time you have available** to successfully sample all of the sampling points. This might be constrained by model assumptions, such as ensuring closure assumptions are met, or by practical constraints, such as the urgency of the study or the availability of personnel. If you have fewer cameras than there are sampling points, then you will obviously need to move the cameras around. The last piece of the puzzle, therefore, is to estimate how long it will take to **install cameras, move them, and collect them in**.

Consider, for example, that your sampling design requires the sampling of 100 point locations for 30 days, all within a single season of ~5 months (150 days). This could be for modelling occupancy of a relatively common and detectable species, with covariates in the model. Imagine that 6 cameras can be installed or collected in a single day, but that double the amount of time is needed if cameras are being moved (i.e. 3 cameras per day). We know that 100 camera traps will be sufficient to complete this survey, and we can probably guess that 10 camera traps will not be enough, but what about 20, 30, or 40 camera traps? By simple book-keeping, you can calculate how many days it will take you to complete the survey with a given number of cameras. For example, if you had 20 cameras, then you know you would have to sample the 100 points in five different blocks, moving the cameras after 30 days each time. In addition, it would take a minimum of 40 field days to install, move and collect in cameras (more, with rest days). This means that it would take you a minimum of 190 days to complete the survey, exceeding the maximum of 150 days. Applying these simplistic calculations for different numbers of cameras, suggests a minimum requirement of 34 cameras (**Fig. 8-1**). Of course, this is a highly simplistic characterisation of real field work, neglecting necessary rest days, as well as likely delays due to bad weather, logistical problems, and camera failure (e.g. malfunction or theft). Given this, the actual requirement may be 15-20% higher, which means ~40 cameras in this case. These "surplus" cameras can be used to help fill any gaps in sampling due to camera failure, and can also be substituted in when cameras become broken or are stolen.

Figure 8-1. An example of calculating the minimum number of camera traps required for a study. The plot shows the total number of days it takes to sample 100 points for 30 days, as a simple function of the number of camera traps available. Note, this calculation assumes that the time required for installation and collection of camera traps is constant across all points and across time, and does not take account of required rest days and likely delays in field work due to external factors.

8-5 Comparisons of camera trap models in the literature and online

Relatively few scientific studies have experimentally tested different camera trap models against each other. In part, this is because camera trap models are changing so rapidly that a study will often be out of date before it is even published. Just three studies have tested camera traps in the laboratory. Swann *et al.* (2004) used a small ceramic heat source to highlight the markedly different detection capabilities of six early camera trap models. Weingarth *et al.* (2013) used a lynx hide containing a hot water bottle to show the inadequacy of infrared flash for obtaining clear images of lynx spot patterns. Meek *et al.* (2014b) tested the sound and infrared emissions of 11 camera trap models, confirming that camera traps produce sound within the hearing range of many animals, and that there is marked variation between cameras, even of the same exact model. In field tests of different camera trap models, Kelly & Holub (2008) found that a Trailmaster active infrared sensor system was outperformed by passive infrared systems, whilst Hughson *et al.* (2010) found evidence of the hit-and-miss nature of passive infrared sensors, as well as variation among cameras even of the same model. Wellington *et al.* (2014), also in field tests, found much higher detection rates of small mammals using Reconyx HC600 camera traps, as compared to Cuddeback Capture IR camera traps mounted concurrently side-by-side.

Trailcampro.com
www.trailcampro.com/pages/trail-camera-tests

Yahoo camera trap e-mail list
uk.groups.yahoo.com/group/cameratraps

Facebook Wildlife Camera Trapping group
www.facebook.com/groups/383092015080952

Camera Traps group on Wildlabs
www.wildlabs.net/community/group/camera-traps

No website currently exists to provide independent and comprehensive comparisons of different camera trap models. The commercial outfit Trailcampro.com have thoroughly tested a large number of camera traps using their own methods, and provide some of the most recent results on their website. However, the methods used are proprietary, and the raw data is unavailable to the camera-trapping community. The website is a very useful source of information, but it should be corroborated with an independent source if possible. Active communities of camera-trappers to ask for feedback can be found on the Yahoo camera trap e-mail list, on the Wildlife Camera Trapping Facebook group, and in the Camera Traps group on Wildlabs.net.

The best examples of highly effective camera trap studies often involve an iterative process of testing and refinement of the methods. Collecting pilot survey data is an invaluable part of this process.

Image of a Siberian ibex, *Capra sibirica*: © Nathan Conaboy / ZSL

9

EXECUTING A CAMERA TRAP SURVEY IN 10 STEPS

Camera trap surveys are hugely variable, in terms of their aims, budgets, constraints and field environments, which makes it difficult to give prescriptive advice on how exactly to plan one. Nonetheless, all ecological surveys should follow a **series of logical steps** in the best-case (**Table 9-1**), if they are to be an effective and wise use of scarce conservation resources. Changing circumstances may often threaten to cut short or derail this series of steps (sometimes successfully doing so), and so you should be prepared, if necessary, to modify or re-arrange these steps to some degree. However, having a clear idea of what you are at least aiming for will allow you to better deal with any challenges along the way.

Step	Considerations	Relevant Chapters in this guide
1. Define clear aims, objectives and constraints	• Your budget is a key constraint, and will in large part determine how ambitious your objectives can be • The time and technical capacity available are also vitally important	**Chapter 7-1**: establishing the "what" and the "why" of a study
2. Design the survey and field protocols	• Plan the logistics for the field work (e.g. travel to study sites, accessing sampling points) and draw up your ideal sampling design • Ideally, the design should be informed by simulated data, or data obtained from another similar study • Simulated data can be analysed to make sure that the design will achieve its objectives (e.g. yield sufficient sample sizes and-or sufficient statistical power to investigate differences)	**Chapter 7**: see relevant part, depending on the specific objectives
3. Establish data collection, management and creation protocols	• Analysing some simulated or test data will focus your mind on the necessary inputs to modelling (e.g. species detections, sampling effort, and covariates) and how they will have to be formatted • Working backwards, this will help you draw up a logical and efficient way of recording field data • This will also help you design a workflow for the camera trap images or videos, specifying how the information in them will be extracted, stored and backed up, and what software will be used	**Chapter 11**: managing camera trap data **Chapter 12**: analysing data
4. Obtain necessary equipment and carry out testing	• Only after completing all the previous planning steps, should equipment be purchased, otherwise scarce resources could be spent on sub-optimal equipment • Once equipment has been purchased, spend some time informally 'playing' with it, to understand its strengths, weaknesses, and how to get the best out of it • If necessary, compare the detection zones of different camera trap models or individual camera traps, to understand any biases that could be introduced into your data	**Chapter 8**: what camera trap to buy **Chapter 10**: realistic expectations to have of camera traps, and what accessory equipment you might need

Step	Considerations	Relevant Chapters in this guide
5. Collect pilot data and analyse it	• All studies should collect pilot data and analyse it, but this is all too often neglected • Up to this point, your entire study is theoretical, and confronting reality with theory is essential for checking if the objectives are likely to be achieved	**Chapter 12**: analysing data
6. Refine the survey design and field protocols	• Pilot data collection and analysis will likely cause you to modify your original sampling design, for the better • Crucially, if pilot work suggests your objectives will not be met, then do not press on with the full data collection regardless; you must instead re-evaluate your aims and objectives • Note, it is sometimes possible to refine the survey design and field protocols mid-way through a study, but this requires very careful thought and, usually, advanced analysis; it is best avoided by careful design at the outset!	**Chapter 7**: designing your survey
7. Carry out the survey in the field	• This aspect of the survey – the fieldwork – may only be a small percentage of the total time and effort required overall!	**Chapter 10**: camera-trapping in the field
8. Catalogue and store the camera trap data	• Extracting information from thousands of camera trap images or videos is a laborious process, and can easily be as time-consuming as the actual fieldwork • Apparent shortcuts to processing data, such as employing citizen science volunteers or machine learning algorithms, may be initially costly to set up and validate • Due attention should be given to proper storage of the data, so that it can be searched and retrieved easily, and so that it is not vulnerable to loss	**Chapter 11**: managing camera trap data
9. Analyse the data, make inferences and produce outputs	• If the study has been well planned and executed up to this point, analysis may be a relatively straightforward process • For non-standard survey designs, or otherwise complex datasets, this may be a time-consuming step	**Chapter 12**: analysing the data
10. Feed the outputs into evidence-based conservation and management	• This is the reason you started the whole process, and it is vital that everything you discovered is recorded for posterity, communicated widely, and learned from	

Despite the great potential of camera traps, there are a number of significant challenges involved in working with them. This can be frustrating for first-time users of the technology and can lead to wasted time and resources. Here we provide some guidance on effective camera-trapping field methods.

Image of camera traps set to monitor gentoo penguins, *Pygoscelis papua*. © Fiona Jones

10 CAMERA-TRAPPING IN THE FIELD

HIGHLIGHTS

- There are three main types of battery compatible with commercial camera traps, with important differences for how your camera trap will perform
- In most cases, nickel-metal hydride (Ni-MH) batteries are the best option, since they are rechargeable; alkaline batteries should be avoided, whilst lithium batteries should be used when it is essential that camera traps operate unsupported for the longest periods possible
- Memory cards with capacities of 4-8 GB and class ratings of 4 or higher should suffice in many cases; at least twice these capacities will be needed if: you are using video mode, your camera traps have high-resolution sensors, or you expect a lot of activity (or misfires) at a given sampling location
- Camera traps should be cleaned and dried between deployments, and stored in a low humidity environment with the batteries removed
- You should fix your camera trap to something sturdy in the field (e.g. a tree or post), 2-3 m from the targeted area and with the sensor 20-50 cm off the ground (< 2 m and < 20 cm, respectively, if small mammals or birds are the focus)
- Camera traps should be directed perpendicular to the expected direction of animal travel (or 45° if camera-trapping at close range, such as on a trail) and angled so that the sensor is aimed parallel to the ground surface; ensure proper setup by using the testing mode on your camera trap or by taking test pictures
- The use of attractants (baits and lures) is not recommended in formal camera trap surveys, unless there are very compelling reasons to use them and it is possible to control for their effects on detection probability
- Theft and vandalism is a common problem during camera-trapping, and can be mitigated by engaging with local communities and informing them of the study, and by either locking your camera traps securely in the field or by making them harder to find (e.g. using camouflaging)
- A wide range of animals (from ants to elephants) will attack and damage camera traps left in the field, and this can be reduced by: encasing your cameras inside protective casing, using cameras with no-glow flash, minimising the amount of scent left behind on and around the camera trap, and using odourless insecticide
- Forest canopy habitats are a promising new arena for camera trap monitoring, but deploying cameras at height presents a number of substantial practical challenges which must be overcome to do it safely and effectively

In previous Chapters, we have covered much of the theory of camera-trapping, including how a camera trap works, how to design your sampling and what features to look for when buying camera traps. However, we have not covered the practicalities of camera-trapping in the field, including what to do when things go wrong (which they will). The day-to-day practicalities of camera-trapping will vary hugely from one study to the next, but there are a few topics which every camera-trapper should know about (e.g. the differences between types of battery), and we cover them here. In addition, we provide potential solutions to common problems encountered in camera-trapping studies, and flag up which ones you are most likely to encounter depending on the type of environment you are working in.

10-1 What type of batteries to use

Almost all commercial camera traps now take AA batteries (some older camera traps took D- or C-cell batteries), and there are therefore three main types of battery technology at the disposal of camera-trappers today: **alkaline, nickel-metal hydride (Ni-MH) and lithium.**

10-1-1 Alkaline batteries

Alkaline batteries are the cheapest and most widely-available type of battery. In storage, they hold their charge very well (for as long as 10 years), and they are nominally capable of providing high voltages (> 1.5 V). You might therefore expect them to perform well in camera traps. However, power-hungry devices like camera traps, which draw high currents for short periods of time, cause alkaline batteries to quickly lose their voltage (see **Fig. 10-1** for an example discharge curve). As a result, the flash on an infrared camera will become noticeable weaker over the course of a deployment, gradually reducing the effective detection distance of the camera at night. In addition, once the batteries are unable to provide the voltage necessary to power the camera – typically 6 V – it will shut down completely, even though the batteries may still have a large amount of their charge remaining (you might find, for example, that the batteries have sufficient charge to power a torch for a considerable time). Alkaline batteries also perform poorly in extreme temperatures (they are effectively useless below -5 °C), and they contain toxic substances that are difficult to recycle and should not be sent to a landfill. For these reasons, **alkaline batteries should be a last resort** for camera-trapping, and are only ever suitable for short-term deployments.

10-1-2 Nickel-metal hydride (Ni-MH) batteries

Ni-MH batteries are more expensive than alkaline batteries (typically about three times the price) but, crucially, they are **rechargeable**. This makes them more cost-effective than alkalines for longer-term monitoring, as well as creating less environmental waste. Ni-MH batteries also hold their voltage at a near constant level during use, meaning that flash output is also maintained consistently until the battery is nearly exhausted (**Fig. 10-1**). They perform very well in extreme cold temperatures (even below -10 °C) and contain only low levels of toxic substances.

However, their nominal voltage is 1.2 V, which may not provide enough power for the most demanding camera traps. Manufacturers typically design their cameras with single-use 1.5 V batteries in mind, which means that they set a minimum voltage for the camera to remain on (such as a cutoff of 5 V) which Ni-MH batteries cannot meet (e.g. four 1.2 V batteries will only put out 4.8 V). You might therefore find that in the user manual for a given camera trap model it states that Ni-MH batteries are not supported. If this is the case, it is still worth investigating if Ni-MH batteries might nonetheless work. In some cases, using Ni-MH in an unsupported model might just mean a slight decrease in performance (specifically a reduced flash range). In other cases, it may mean the camera could power off unpredictably. You can

Trailcampro.com
www.trailcampro.com

check online to see if others have had success using Ni-MH batteries with a given camera trap model (e.g. Trailcampro.com provide this information for cameras that they test).

Ni-MH batteries also do not hold their charge very well. Typically, they will lose 10% of their charge in the first day after charging, and then approximately 1% per day after that. This means that, even if a camera trap does not take a single picture, a battery life of more than 3 months is rarely achieved with Ni-MH batteries. These self-discharge rates are even worse in high temperatures, and may be as high as 5-15% per day. Under daytime temperatures of 40 °C or more, battery life might be as little as 1-2 weeks. **Low Self-Discharge (LSD)** Ni-MH batteries are a variant of Ni-MH batteries with much improved self-discharge rates. They are more expensive than normal Ni-MH batteries though, and are typically lower capacity (up to a maximum of 2500 mAh, compared to 2800 mAh for standard Ni-MH batteries). LSD Ni-MH batteries are marketed under various names, such as “pre-charged” or “ready-to-use”, and are now available from a range of manufacturers (the most well-known being Sanyo’s Eneloop brand, the first manufacturer to produce them).

There are also maintenance costs associated with using rechargeable batteries. Specifically, they must be properly charged, tested and stored. Ni-MH batteries should only be charged with so-called **“smart” chargers**, which are able to monitor the charge of individual batteries and avoid damaging them by overcharging. Ni-MH batteries do not have a strong “memory” effect (a reduction in the capacity or voltage due to partial discharging), like the old nickel-cadmium (Ni-Cad) batteries did, but they can nonetheless benefit from 3-4 discharge-recharge cycles if the voltage noticeably declines. Some battery chargers have a “refresh” or “reconditioning” mode for carrying out these discharge-recharge cycles, but it can also be done manually (you can use an LED torch to run the batteries down). Battery voltages can be checked using a battery tester (i.e. a small, handheld voltage meter), but a rough guide might be to refresh your batteries approximately every 10-12 uses. Depending on how intensively you use your batteries, you can expect to get 3-5 years of usage before the voltage declines irreparably. Try not to mix batteries in your camera traps which have very different charge levels, as the more highly charged batteries can cause a permanent polarity reversal in batteries with a lower charge (particularly in older camera traps which do not guard against this). If you are storing your rechargeable batteries for a prolonged period of time, note that it is best to store them with at least 30% of their charge, so that they do not completely discharge.

Despite some of the drawbacks of Ni-Mh batteries, **in most cases they are the best option** for camera trap studies. Look for high-capacity Ni-MH batteries (at least 2500 mAh), and especially LSD Ni-MH batteries, for the best results with rechargeables.

10-1-3 Lithium batteries

Lithium batteries easily give the **best performance and battery life**, and can power camera traps for 6 months or longer. They have a nominal voltage of 1.5 V (in practice often giving out 1.6 V), they maintain a consistent voltage output during use (**Fig. 10-1**), and they have very low self-discharge rates. Lithium batteries also perform well in extreme heat and cold (even below -30 °C) and contain low levels of toxic substances should they enter a landfill. However, lithium batteries are expensive (as expensive as Ni-MH batteries) and cannot be re-used, making them especially costly for long-term monitoring.

Due to their expense and environmental waste, lithiums are a second choice behind Ni-MH. They should be considered for specific cases when Ni-MH batteries will not suffice, such as when cameras cannot be serviced frequently or for maintaining high-drain networked cameras.

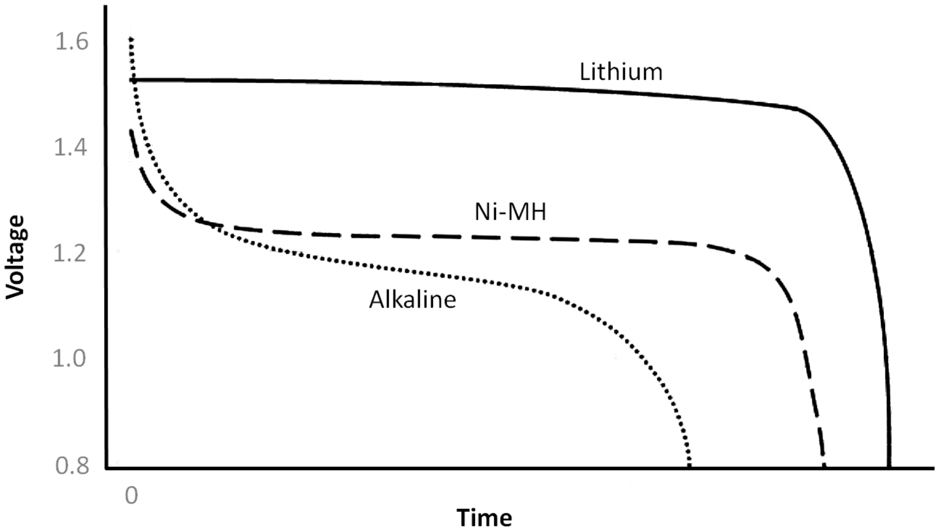


Figure 10-1. Example battery discharge curves for the three main types of AA battery currently used in commercial camera traps. Real data may show considerable variation around these idealised patterns. Adapted from van Berkel (2014).

Some manufacturers (e.g. Spypoint) now produce rechargeable lithium-ion battery packs (as used in mobile phones and laptops) for their camera traps, which slot into the AA battery trays. Lithium-ion batteries are a completely different type of battery to lithium batteries, which are single-use only, but will offer similarly high performance.

10-1-4 Other options for powering your camera trap

If you need to power a camera trap for more than a few months, or if you're using power-hungry networked camera traps, then you may want to consider upgrading from just using AA batteries. To do this, you will need a camera with an **auxiliary power jack** (check the manufacturer's specifications), or you will need specialist electronics knowledge to "hack" the camera. In either case, it is possible to power the camera using a high-capacity **lead-acid battery** (6 V, 9 V or 12 V, depending on the camera), more commonly used for boats and cars. These rechargeable batteries come in a range of different capacities depending on how much battery life is required, and they are relatively cheap. However, they are heavy and must be recycled carefully due to the lead that they contain. Some manufacturers sell weather-sealed lead-acid batteries specifically designed for their camera traps (e.g. Spypoint and Moultrie).

The alternative option for remote deployments is to use a **solar panel**. These can be attached to a power jack, and also come in a range of sizes depending on your requirements. You will need to check if the solar panel is compatible with your camera (particularly, if the voltage is correct and if the power cord will actually plug into the camera). Various camera trap manufacturers sell solar panels specifically for their camera traps (e.g. Acorn, Bushnell, HCO, Reconyx, Spypoint etc.), which circumvents any compatibility issues. Spypoint also have a camera trap (the Spypoint Solar) which has an integrated solar panel module attached to it, which is capable of charging under indirect sunlight.

For deployments closer to base, or in urban areas, it is also possible to use mains power. Mains power is alternating current and must first be converted to direct current before being plugged into a camera trap.

Note that, besides being expensive and bulky to transport, using an external power supply is also likely to make your camera trap more conspicuous and liable to theft.

10-2 Memory cards

Almost all commercial camera traps use **SD (Secure Digital) memory cards**, which come in two main forms: standard (SD) and high-capacity (SDHC). SD cards have a maximum memory capacity of 2 GB, whilst the newer SDHC cards can have a capacity up to 32 GB. Some older camera traps may not work with SDHC cards, or may only work with SDHC cards up to a certain capacity, so check the user manual for your camera trap. There is also a third type of SD card with capacities up to 2 TB – the extended-capacity (SDXC) card – but these are not yet compatible with most camera traps.

Since they have small image sensors, commercial camera traps produce relatively low resolution images with a small file size (compared to DSLR cameras). This means that the highest capacity SD cards are not normally necessary. Assuming images with a size between 400 KB and 900 KB (this varies depending on the resolution of the camera and the colours present in each image, with black-and-white night images being smaller in size), a 4 GB card will be able to hold between 10,000 and 4,000 images, respectively. This should be sufficient for most short- and medium-term deployments (< 4 weeks), but will depend on how much activity and how many misfires occur at a given sampling point. For long-term deployments (> 4 weeks), you will likely want to use a card with at least 8 GB of memory, capable of storing 8,000-20,000 images (assuming images 400-900 KB in size).

Some of the newer camera traps record high-resolution images (of 10 Megapixels or higher), usually by interpolating the image from a low resolution compact sensor. These produce much larger images (~ 2 MB), and larger memory cards will be required in this case. You will also want much larger memory cards if you are using a video mode: at least 8 GB for short- and medium-term deployments, and probably up to 32 GB for long-term deployments (assuming battery life can extend that far in video mode).

SD cards vary not just in terms of their capacity, but also in terms of the speeds at which they can read and write data. The write-speed is particularly important for camera-trapping, as slow speeds could lead to poor performance in cameras with near-video modes or those that record high-definition video. The SD card "class" indicates the speed at which it can read and write data (classes 2, 4, 6 and 10 are common options available), and **you should use class 4 (or higher) SD cards** with camera traps. Memory cards also vary in their build quality, and it is a good idea to buy a reliable brand (e.g. SanDisk).

Memory cards may look like pieces of plastic, but they contain circuit boards, and it is good practice to treat them delicately to reduce the chances of them failing on you (usually at the worst possible moment). They should not become wet, or be compressed or bent. Make sure your memory cards are free of dust and dirt (especially the metal contacts) when you insert them into any camera trap, otherwise your camera may experience problems reading and writing to the memory card. You should also be aware that SD cards have a write-protection switch, to allow you to prevent the data on it from being recorded over. This switch (usually on the side of the card) should be kept in the unlocked position, to avoid any problems.

It is good housekeeping to **regularly format your memory cards**. This will lead to improved performance by freeing up the maximum space available on the card (this can decrease over time, as the memory becomes fragmented with use) and usually also giving you faster write speeds. Formatting can be done with a computer, and is also available on some camera traps.

Wi-Fi SD cards, which can send images to a computer, tablet or mobile phone, are also available (e.g. Eye-Fi brand), but these will likely not work with your camera trap. Wi-Fi cards require that your camera remains powered on after taking an image for a sufficient amount of time to send the image over a Wi-Fi network. Most camera traps, however, immediately enter a sleep mode to save battery.

10-3 Camera trap storage and maintenance

Like any other electronic devices, camera traps require care and attention if they are to work effectively, especially given repeated and prolonged exposure to wet, muddy, sandy or salty conditions. Camera traps should be kept clean and dry between deployments, with the batteries removed (to prevent batteries from leaking inside the camera). In hot and humid environments, dehumidifiers or air-conditioning can be used, if available. This will help dry out cameras between deployments, and will also help to prevent the growth of fungus in the longer-term. Care should be taken to bring camera traps back to outside temperatures inside a sealed bag to avoid condensation forming inside the electronics. A well-ventilated cabinet with a standard lightbulb (not an energy-saving bulb) inside is also a good place to store camera traps in humid environments.

In camp conditions, watertight boxes (e.g. Pelican cases) filled with silica gel packages can be used to temporarily store camera traps during field work. However, the silica gel packages should be regularly dried out (e.g. in a field oven on low heat) in order for them to be effective.

Before each major deployment, it is good practice to systematically prepare each camera trap, by inspecting it, cleaning it and testing it (sometimes cameras can develop problems during storage). Any damage or malfunctioning should be recorded in a spreadsheet (**Chapter 11-1-1**). Finally, the memory card should be formatted and the batteries, if you are using Ni-MH, should be fully-charged.

10-4 Where and how to mount your camera trap

So you arrive at your camera trap location, with a fully-charged camera trap ready-to-go. Your next challenge is how exactly to fix the camera trap in the environment such that it is secure and will detect animals in the most effective way possible. Unfortunately, this is not as simple as just tying it to a tree and letting it do all the work.

10-4-1 Choosing a suitable microsite for your camera trap

If you are doing a formal camera trap survey, you will likely have navigated to a GPS point in the field. This is your starting point and, from there, you must find a suitable place to focus your camera trap on. Depending on your sampling design (see **Chapter 7**), you may have some amount of flexibility to deviate from the GPS point, but in most cases **the closer you can place the camera to the GPS point the better**. Note that handheld GPS units are usually accurate only to within 5-20 m (depending on satellite reception), so make sure you have a repeatable and objective rule for determining where your final GPS point should be (e.g. take the first location it indicates is zero metres from your desired waypoint and ignore any subsequent deviations).

For random placement (the preferred strategy for almost all study objectives), the main concern is to **avoid microsites with major obstructions** which will block the camera's field of view, such as rocks, tree buttresses or uneven ground surfaces. In dense vegetation, it is usually necessary to clear a small amount of vegetation, but you should keep this to the minimum possible; many animals will notice the disturbance and may alter their behaviour. If your sampling design allows a bit of extra flexibility (e.g. under a grid-based occupancy design; see **Chapter 7-9-2**), then you may want to find the **nearest focal point of animal activity**, such as a trail. However, you should be aware that you may have to restrict your inferences only to these focal points of activity, unless you can account for it in your modelling approach (for example, by including a covariate in your occupancy models).

For dedicated capture-recapture surveys, your best option is often to try to **maximise capture probabilities** of your focal species. This may come at the cost of increased heterogeneity in capture probabilities, possibly leading to biases in density estimates, but may be necessary in order to obtain any density estimate at all (see **Chapter 7-7** for more information). For inventory work, where the aim is simply to detect as many species as possible, targeted placements to maximise detection probabilities are also justified (**Chapter 7-4**). Using your knowledge of the natural history of your target species, you may decide to focus your camera traps on major trails, roads and ridge-lines (e.g. for big cats, which often prefer to take the easy route), or on burrows (e.g. armadillos and badgers), tree-holes (e.g. pangolins and possums) and other focal points of animal activity (e.g. latrines, for otters).

10-4-2 Fixing your camera trap in the environment

Once you've identified the microsite you want to focus your camera on, you'll now need to securely attach your camera trap to something in the environment. Trees make great camera trap posts, and in a forest environment they're abundant and free. Make sure the tree you choose is still alive and not liable to falling over at any moment, and that it is sturdy enough to remain stationary in windy weather (if your camera is not completely static, you will likely get many blank images). Also make sure it does not have any ant or termite nests in it; you do not want your camera trap to become part of the colony!

If there are no trees nearby, or if your environment is treeless, you will need to bring something with you to fix the camera trap onto (**Fig. 10-2**). You may be able to cut tree poles (> 10 cm diameter-at-breast-height is best), or you can use wooden stakes (typically used for fencing). Metal poles can also be used, but they are heavy and expensive. Some camera manufacturers sell metal poles specifically for this purpose (e.g. Cuddeback). A more compact option is to use a ground spike (with an integrated attachment for the tripod thread present on most camera traps; e.g. see www.wildlifewatchingsupplies.co.uk). The main thing is that your camera trap post is **sturdy enough** to remain stationary in the wind, and sturdy enough for animals to brush up against without it falling over (in open environments, you may find that herbivores use your camera trap as a scratching post!). If you are protecting your camera against thieves, your post will also need to be securely fixed into the ground (**Chapter 10-6**).

Figure 10-2. Fixing camera traps in the environment when trees are unavailable. In the Serengeti plains, metal posts and steel security boxes were used to help guard against attacks from elephants and hyenas (**A**, from Swanson *et al.* 2015). In Mongolian steppe habitat, wooden stakes hammered into the ground were sufficient for mounting cameras in the environment (**B**).

The tree or post you are using should be positioned at an appropriate distance from the microsite you are focussing your camera trap on. In most cases this will be a **minimum of 2-3 m**, in order to obtain a sufficiently wide field of view and in order to give your camera trap sufficient time to trigger and record an image or video. For example, if you are focussing your camera trap on a trail and place your camera too close, an animal may enter and leave the camera's narrow field of view before your camera can react and capture the action. If you are using a camera trap with a slow trigger time (> 1 second), or you are using a video mode (typically requiring a trigger time of > 2 seconds), then a minimum distance of 3-5 m will be more effective. If you are targeting **small animals**, for example at a bait station, then closer **distances of < 2 m are recommended** (Rowcliffe *et al.* 2011; Paull *et al.* 2012; Mills *et al.* 2016). If greater distances are used, animals may not trigger the sensor or may not be large enough in the image to allow for identification. Note that these distance recommendations apply to camera traps with an integrated passive infrared sensor. If you are using a separate camera and sensor (e.g. a camera paired with an active infrared sensor or separate passive infrared sensor), then there is much more flexibility on where exactly you place your camera and your sensor. For example, you could focus your sensor on wherever you expect the most activity, but place your camera wherever the field of view is greatest.

Most camera traps come with straps or bungee cords for tying your camera to a tree or post. Note that bungee cords may cause your camera trap to gradually shift during long deployments. If you are protecting your camera against thieves, you may be able to directly use a cable lock to secure your camera to the tree or post, instead of using a strap (check if your camera trap has a compatible case; for example, all Reconyx camera traps contain a recess for a cable lock).

An alternative option for attaching your camera trap to a tree or post is to use a dedicated **camera mount**. These screw into the tripod thread on the back or underside of most camera traps, and then attach to a tree or post using screws or bolts. They usually have a ball head or some other adjustment mechanism, to assist with aiming your camera. Most camera manufacturers sell these camera mounts (e.g. Cuddeback, Bushnell, Moultrie, Reconyx, Spypoint, UWAY etc.), and these should all work with almost any camera trap, provided it has a tripod thread. Third-party manufacturers also offer camera mounts which will work with most camera traps (e.g. Custom1 Enterprises and Slate River).

10-4-3 Focussing your camera trap on a target height and direction

Once you have chosen the microsite you are interested in monitoring, and the tree or post you will use to secure your camera, there are two final parameters to consider when setting up your camera trap: **camera height and camera direction**. Although poorly explored experimentally, experienced camera-trappers will tell you that proper aiming of a camera trap, both in terms of its height and direction, will have a large impact on the number of detections obtained. Passive infrared sensors do not function in the way most researchers imagine (see **Box 4-1**) and it is easy to set them up in an ineffective way.

Camera trap manufacturers make recommendations on camera height for obtaining nicely composed images of large deer, and this means setting cameras at 1.5 m (e.g. the Reconyx Hyperfire manual). However, in almost all cases you will want to use a much lower height for wildlife research. A sensible recommendation is to aim for a distance of **20-50 cm between the camera sensor and the ground** in order to detect a wide range of small, medium and large animals (e.g. O'Brien *et al.* 2003; Tobler *et al.* 2008; Kays *et al.* 2011; Wearn *et al.* 2016). Only the bottom half, or only the legs, of the largest animals may be visible in images if they are close to the camera, but in most cases this will not be a problem for species identification. For targeting small animals only (e.g. small mammals and birds), it may be advisable to position the sensor even lower, at 10-20 cm from the ground (Thornton *et al.* 2012).

For targeting a single species (e.g. in a capture-recapture study), you can set your camera trap sensor at the approximate **shoulder height of your focal species**, or the height at which your species emits the most infrared radiation (i.e. heat). Many vertebrates consistently emit infrared from their heads (because their sensory systems must be exposed to the air), but this can vary across species and across time (Kuhn & Meyer 2009; Meek *et al*. 2012; Cilulko *et al*. 2013). Silver (2004) recommended a sensor height of 50-70 cm for jaguars, whilst Mohamad & Darmaraj (2009) recommended 40-50 cm for tigers. Some animals will notice the faint red glow emitted by “low glow” (near-infrared) flashes if a camera trap is at their eye level. If this is a significant problem for your study, you can set cameras higher up and facing downwards, but this will likely reduce the size of your detection zone.

Only two studies have investigated the effects of camera trap height to date. Swann *et al.* (2004) compared detections of animals models (hot water bottles and human subjects) made at 20 cm and 120 cm by a range of camera traps that were in use at that time (e.g. TrailMaster, CamTrakker and DeerCam units). They found that the small mammal models were poorly detected by cameras set at the higher height of 120 cm (Swann *et al.* 2004). Meek *et al.* (2016b) found significantly lower detection rates for Australian medium- and large-mammals when modern Reconyx camera traps were placed at 350 cm compared to 90 cm.

To most effectively exploit the characteristics of a passive infrared sensor, it is best to face it **perpendicular to the expected direction of animal travel**. This will maximise the amount of side-to-side motion that the sensor will “see” and make it more likely to register a detection (see **Fig. 4-2**). If you set up a camera trap sensor facing head-on towards the direction of travel, you may find that animals exhibit little side-to-side motion and that they are poorly detected. You will also find that fewer animals will react to your camera trap if it is set up perpendicular to their direction of travel, as they will be less likely to see it and less likely to notice the flash.

If you are camera-trapping a narrow trail in dense habitat then it can be difficult to place your camera sufficiently far from the trail to get an unobstructed view of a decent length of it (without disturbing a large amount of vegetation). In this case, it is often more effective to face your camera at a 45° angle to the trail, rather than facing it perpendicular (**Fig. 10-3**). This will give your camera trap a view of a greater length of the trail and give it more time to react and capture any animals walking along it. If you are using a setup with a separate camera and sensor (e.g. a camera paired with an active infrared sensor or separate passive infrared sensor), then there is much more flexibility on where exactly you place your camera and your sensor. In this case, you could deploy your sensor close to the trail and place your camera further back, or at an angle, to maximise the field of view.

In addition to angling your camera correctly from side-to-side, you will likely also need to adjust the vertical angling as well. Camera trap sensors vary greatly in their characteristics, but in most cases you should adjust the vertical angle of your camera trap so that it is **perpendicular to the ground surface in front of it**. If you are camera-trapping on a slope, this will mean you will have to angle your camera downwards (if facing down a slope) or upwards (if facing up a slope). It is usually better to have a camera trap facing slightly downwards than a camera trap facing up to the sky; the former may shorten the detection zone, leading to missed detections at longer ranges, but the latter may mean that no part of the ground in front the camera is monitored effectively.

Figure 10-3. Camera trap setup along trails. Cameras should be set back 2-3 m from the trail in order to give the camera sufficient time to react and record images of any passing animals. Setting the camera at a 45° angle to the trail (as in **A**) will also give your camera more time and provide a view of a greater length of the trail. Examples images are from Madagascan rainforest (**A**) and Brazilian cerrado (**B**; © Guilherme Ferreira).

Figure 10-4. Making fine adjustments to the aim of a camera trap. In steep areas it will often be necessary to angle your camera downwards or upwards to run parallel with the ground surface. If you are not using a dedicated camera mount, short sections of wood, wedged behind the camera trap, are an effective and low-cost alternative (**A**). If you are using trees or other natural objects to mount your camera traps, it will often be necessary to make fine adjustments to the angle, even if the terrain is relatively flat (**B**). Again, short pieces of wood or rock, firmly wedged behind the camera, can be used.

Camera mounts (**Chapter 10-4-2**) allow for easy adjustment of the vertical angle, and some camera traps have an integrated angle adjustment mechanism on the casing (e.g. Browning camera traps). Otherwise, you can use any kind of wedge pushed in behind the camera (**Fig. 10-4**), to lever it upwards or downwards as necessary. If you know you will be camera-trapping a particularly steep area, then you can cut small lengths of wood (10 cm) in advance and bring them for this purpose. Using dead wood found in the environment is not advisable for longer deployments, as it will decompose and disintegrate.

Once you have set up your camera trap, you should test it. Almost all camera traps with a passive infrared sensor have a **testing mode** specifically for this. When your camera is in this mode it will give you feeback when the passive infrared sensor has registered a detection – typically with a flashing light on the front on the unit – without recording any images or video. A quick way to test it is to approximate a medium- to large-sized mammal and crawl in front of the camera, testing it from different directions and different distances (**Fig. 10-5**). The infrared signal emitted from a human is typically strongest from the head area, so crawling will allow you to better approximate the infrared signal of most mammal species than walking. However, if you are targeting a large species, with a shoulder height greater than 1.5 m, then walking will be more effective. Some camera traps also have an integrated laser pointer which can give an indication of where the camera's detection zone is centred.

You can also take some test images and view them, either on the camera trap's viewing screen (if it has one) or a separate device. Some camera trap manufacturers sell dedicated image viewers, usually with rugged, all-weather designs (e.g. Cuddeback, Moultie, Spypoint etc.). You should be aware that digital cameras and camera traps do not usually cooperate very well. Camera traps typically place their images into a folder on the memory card, which most digital cameras will fail to find. Some digital cameras will also modify the folder structure on any memory card that is inserted into them, and possibly place extra files onto them, which may mean your camera trap will not work with the memory card (using the camera trap to format the card will fix this, but you will lose all the data on it). The safest way of viewing images is to use a memory card reader (e.g. from Stealth Cam) attached to a computer, tablet or smart phone. Wireless memory card readers are also available (e.g. from Whitetail'R). As a last resort, you can also activate the front camera on your mobile phone (if it has one) and place it against the lens of the camera trap (in landscape orientation). This will give you an approximate view of what the camera trap images will look like.

Figure 10-5. Testing a camera trap in the field to ensure the height and direction is correct for the target species. Crawling is a better method than walking, unless you are targeting species with a shoulder height > 1.5 m.

10-4-4 Last things to do before leaving your camera trap

Before abandoning your camera trap to the wilds, there are a few last things you should do. You should record, at a minimum: the exact time and date that sampling begins; the GPS coordinates of the exact location, and the serial number of the camera (or the custom camera number you may have assigned to it). This is the time also to record any environmental covariates you will use during modelling (e.g. elevation, land-use type, signs of human disturbance, canopy cover, vegetation density etc.). All of this information should, ideally, be recorded into a **pre-prepared data sheet**, so that you do not forget to record anything. You may also want to take a photo of the camera trap in-situ for your records, which may also prove useful in case you have difficulty finding the location at camera pick-up.

Lastly, do a **final check** that the camera is ready to be effective. The camera lens, infrared sensor, day/night sensor and any rubber gaskets on the casing should all be free of dirt and dust. The camera should have sufficient battery and memory to last the deployment. Add any silica gel packets (essential in humid environments) to the interior of the casing just before closing it shut. Make sure you camera is turned on and armed to take pictures before you leave. Some cameras traps will helpfully arm themselves automatically when left inactive in testing mode for a given period of time (e.g. after 2 minutes of inactivity for Reconyx camera traps). It is good practice to **trigger the camera to record an image or video as you leave**, which can serve as a record of the exact date and time the camera trap began sampling.

Figure 10-6. The final check before leaving a camera trap. After mounting and aiming your camera, check that the camera will be able to function as expected (i.e. it is clear of debris on the front of the camera and in any rubber gaskets, and it has sufficient battery and memory). The last thing to do is add any silica gel packets to the inside of the camera before closing it firmly.

10-5 Baits and lures

Many animal sampling methods, such as live traps and hair traps, use baits and lures to attract animals to the trapping station from the surrounding area. This increases the **effective sampling area** of the trap and consequently increases detection probabilities and detection rates. This is a necessity for some sampling methods, because otherwise the chances of an animal bumping into the trapping device are very small (consider the very small effective trapping area of an unbaited live trap). Given that camera traps can have detection zones that are notionally greater than 300 m^2 (Meek *et al.* 2012), it is a realistic proposal to just allow animals to go about their natural movements and sample them at random. Doing this better satisfies the assumptions of most modelling approaches applied to camera trap data (**Chapter 7**). If you would like to use bait or lures to increase the quantity of data you receive into your camera trap, you should be aware that you may be **decreasing the *quality* of the data** at the same time, by violating modelling assumptions and increasing the chances of making biased inferences.

Modelling approaches that, in principle, can accommodate baits and lures include occupancy (using a grid-based design, but not if you want to use a point-based design) and capture-recapture. For example, Thorn *et al.* (2009) used scent and food lures to greatly increase detection probabilities in an occupancy study of brown hyenas, whilst Garrote *et al.* (2012) used food lures to increase capture probabilities in a capture-recapture study of Iberian lynx. Ngoprasert *et al.* (2012) used a hanging food lure to encourage bears (Asiatic black bears and sun bears) to stand on two legs and reveal their individually-diagnostic throat pelage markings. A similar approach using a hanging food lure was taken for wolverines, which also have unique throat pelages (Royle *et al.* 2011).

You should be aware, however, that if baits and lures introduce heterogeneity into your data – for example if responses to the attractant vary by individual, by species and over space or time (e.g. depending on the background food availability) – this **may introduce bias into your model estimates**. It is theoretically possible to control for variation in capture probabilities (e.g. differences based on the sex of an animal) during modelling, but this requires substantial amounts of data, which can often prove difficult to obtain in practice.

A wide variety of baits and lures are used in animal sampling, including audible, visual and olfactory attractants. The most effective option will depend on the species, or set of species, you are targeting, and on the environment in which you are doing it. Baits and lures used in camera trap studies have included commercial scent lures (Belden *et al.* 2007), food lures (Mace *et al.* 1994; De Bondi *et al.* 2010; Royle *et al.* 2011; Garrote *et al.* 2012; Gerber *et al.* 2012; Ngoprasert *et al.* 2012; Paull *et al.* 2012), food baits (Watts *et al.* 2008; Hamel *et al.* 2013; Edwards *et al.* 2014; Fuller *et al.* 2016; Roy *et al.* 2016), animal carcasses (Du Preez *et al.* 2014; Forsyth *et al.* 2014; Newey *et al.* 2015) and even compact disks hung up in trees (Nielson & McCollough 2009). Few studies have rigorously compared different types of attractant, but both Espartosa *et al.* (2011) and Thorn *et al.* (2009) found that food baits were more effective than scent lures for a range of species (in Brazilian rainforest and South African bushveld, respectively). Scent lures have typically just been applied to objects in the environment, such as trees or rocks in front of cameras (e.g. Belden *et al.* 2007; Thorn *et al.* 2009; Espartosa *et al.* 2011), whilst food lures have been either hung up (e.g. Mace *et al.* 1994; Royle *et al.* 2011; Ngoprasert *et al.* 2012) or concealed behind wire mesh (e.g. Gerber *et al.* 2012; Paull *et al.* 2012) to stop animals from removing them.

Some **baits and lures can be expensive** to procure, and usually have to be repeatedly re-applied during the course of sampling. These added equipment and labour costs will have to be budgeted for. Balme *et al.* (2014) also discuss the **possible behavioural effects of using food baits** (and carcasses), which include altered ranging behaviour, increased inter- and intra-specific interactions, and habituation towards food baits. For example, the use of food baits to study leopards could lead to: increased contacts between leopards and lions; infanticide of leopard cubs, and higher numbers of leopards killed by trophy hunters (which also sometimes use food baits).

Overall, **we recommend avoiding the use of attractants in formal camera trap surveys**, unless you are doing an occupancy or capture-recapture study and there are very compelling reasons to use attractants. Perhaps the most suitable use-case for baits and lures is that of the informal inventory survey. In this case, no modelling assumptions have to be satisfied (**Chapter 7-4**) and a variety of attractants can be used to target different species in different microhabitats.

10-6 Combating theft and vandalism

In many parts of the world, theft and vandalism by people will be one of the main challenges faced by a camera trap study. In two extreme examples, Espartosa *et al.* (2011) reported that 25% of their cameras were stolen during camera-trapping in the Brazilian rainforest, whilst Hossain *et al.* (2016) lost > 50% of their camera traps due to suspected theft in the Bangladesh Sundarbans. Thieves and vandals will interfere with camera traps out of curiosity, opportunity and malice, and you will often rarely know which one was the main cause, making it difficult to combat. If you are camera-trapping where illegal activity is occurring, people may also want to destroy any evidence that could have been captured by your camera traps. Approaches to deal with interference by people will vary depending on local context. You are, in effect, trying to modify people's behaviour, which is notoriously difficult to do. You may only discover the most suitable method by trial-and-error.

The most straightforward approach is to **engage with local communities and inform them of the stud**y, its aims, and how they will be affected. This is also a good opportunity to communicate what your policy of dealing with images of people is (e.g. images of people will be anonymised, or deleted immediately). If this is done in concert with awareness-raising campaigns, for example environmental education, you may be more likely to receive a positive response to your study and its aims. It may also be possible to **directly involve members of local communities** in your study, as volunteer citizen scientists or as paid field technicians. This will hopefully encourage even stronger positive attitudes to your camera trap study, albeit from a more limited number of people. You can also inform people about the study in the field, using **signage** at key access points or directly at the camera sampling points (e.g. by attaching a small notice to each camera trap).

This approach of informing and engaging local communities may reduce incidences of theft and vandalism, but is unlikely to stop it completely. Where persuasion fails, theft prevention may be required. This can be achieved using a **cable lock** (compatible with many camera traps) or chain to attach a camera trap to an immovable object (**Fig. 10-7**). These will deter opportunistic thieves, but will not stop determined and well-prepared thieves (e.g. cable locks are susceptible to bolt-cutting tools, or even just a heavy impact from a machete), and will not prevent vandalism. Locks and chains can be combined with **metal security cases** to offer more protection from vandalism. Many camera trap manufacturers sell security cases designed for a specific camera trap model (e.g. Bushnell, Cuddeback, Reconyx, Spypoint etc.), as do third-party manufacturers (e.g. Custom1 Enterprises). It may also be possible in some countries to get customised security cases manufactured at reasonable cost.

Custom1 Enterprises
www.custom1enterprises.com

Figure 10-7. Using cable locks (**A** and **B**) and chains (**C**, © Guilherme Ferreira) to secure camera traps in the field and deter thieves.

The most secure way of installing a camera trap is to combine a security case with a **permanently-installed metal post**, sunk deep into the ground, ideally with concrete (**Fig. 10-8**). The security case can be integrated into the metal post or attached using lag bolts only accessible from within the locked security case.

Figure 10-8. Using custom-made security posts for the highest protection when deployment in high-risk areas is unavoidable. The camera trap is secured within a steel box and bolted or welded onto a steel post, which is then sunk into the ground and fixed with concrete (**A**). The plastic tub is a rain cover for the padlock. If the camera trap is designed to be compatible with a cable lock, it can also be secured within the box by passing a metal skewer through the camera trap's casing (**B**). In combination with the padlock on the outside of the box, the camera is then doubly-secured (**C**).

An alternative to engaging in a costly arms race with thieves and vandals, is to hide your camera traps (**Fig. 10-9**). This can be done with **camouflaging** (e.g. attaching natural materials to the outside of your camera, or deploying it within a recess, such as a tree-hole or amongst rocks). Some manufacturers also sell decoy or "dummy" camera traps (e.g. Reconyx, Spypoint), used to draw attention away from the actual functioning camera traps. Using camera traps with **no-glow (black) infrared flash** will also reduce the chances of them being discovered at night. Perhaps the most effective method of hiding your camera traps, however, is to **alter how you deploy them over space and-or time**. This decision must not be taken lightly, since the inferences you can make may be seriously weakened, or even compromised, if you change your sampling design dramatically (see **Chapter 7** to check the assumptions of any modelling approaches you might want to use). Options for hiding your camera traps in space include setting them high up out of eye-line (e.g. in trees), only deploying them off-trail, or only deploying them on private land with controlled access. Options for hiding your camera traps in time include only sampling at particular times of day (e.g. at night) or particular seasons (e.g. winter) when fewer people are present in the area.

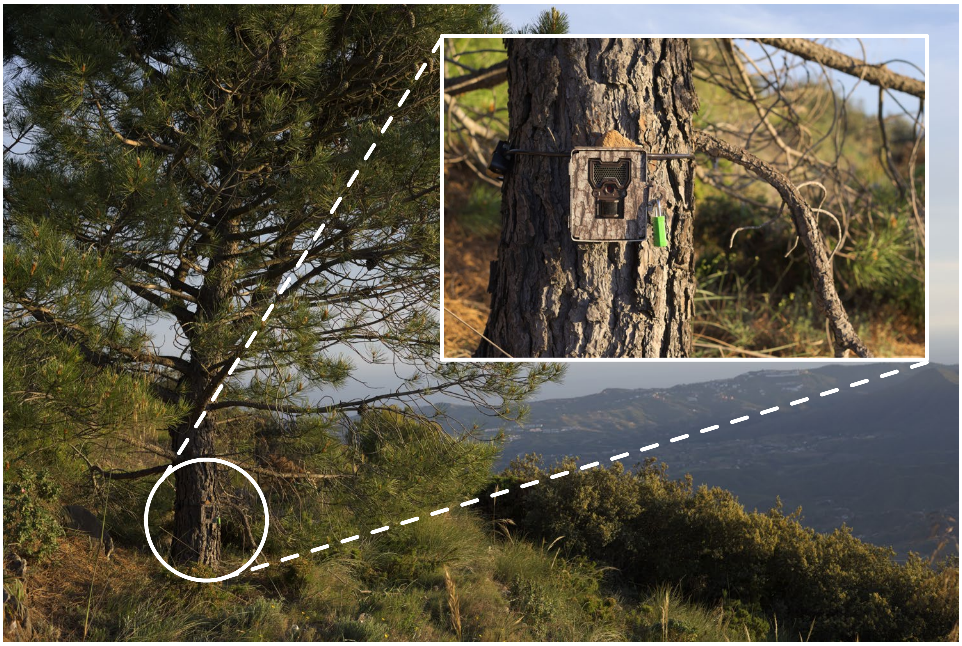


Figure 10-9. A well-camouflaged camera trap can be inconspicuous in the landscape, making it difficult for thieves and vandals to spot. Here, the security casing has been covered in a pine bark camouflage, helping it to blend in with the tree bark.

Some camera traps have anti-theft measures, although these are not usually very effective. For example, it is possible to set a PIN code on some camera traps, which will render the unit useless to any thief. Miniature Bluetooth trackers can be deployed covertly on or inside camera traps (e.g. TrackR), but these have a very short range (< 30 m), which makes recovery very unlikely. GPS trackers are not currently small enough to be deployed covertly on or inside commercial camera traps. Networked camera traps may offer some hope of recovering stolen devices, since they may send images of the perpetrators over mobile phone or Wi-Fi networks before being disabled. The PixController Raptor networked camera trap can be configured to send a message to a mobile phone if the camera starts moving (Meek *et al.* 2012). One proactive approach to combating theft is to set up a covert camera on access points, specifically targeted at identifying people or their vehicles (this approach must be carried out in accordance with local laws).

10-7 Damage and interference from wildlife

Many studies report problems they encountered due to wildlife, either causing damage to camera traps (**Fig. 10-10**) or interfering with their proper functioning. Some species are notorious for targeting camera traps for destruction, especially **elephants** (Karanth & Nichols 1998; Henschel & Ray 2003; Grassman *et al.* 2005; Mohd-Azlan 2006; Mohd-Azlan & Sharma 2006; Rayan & Mohamad 2009). In one study, more than 30% of the camera traps used were destroyed by Asian elephants (Mohd-Azlan & Sharma 2006). Other species reported to be hostile to camera traps include bears (Rice *et al.* 1995; Jordan *et al.* 2011; Ancrenaz *et al.* 2012), porcupines (Gregory *et al.* 2014), rhinos and tigers (Karanth & Nichols 1998). Many primate species are highly inquisitive and may try to open a camera trap or alter its positioning (e.g. macaques). A poorly-reported, but possibly quite widespread, problem is also social insects, including **ants and termites** (e.g. Gregory *et al.* 2014). The inside of a camera trap is a desirable home for some species of ant and termite, and they will collectively chew their way in through any possible access routes, such as the rubber gasket. Once inside, they often cause irreparable damage to the circuit board and other components. Spiders and insects can also build webs and nests over parts of a camera trap which must be exposed, such as the lens, passive infrared sensor or light sensor.

Figure 10-10. Camera traps damaged during long-term monitoring in the Serengeti National Park (Swanson *et al.* 2015, 2016), mostly by hyenas, elephants and fire. Image © Daniel Rosengren.

For dealing with large mammals intent on destroying camera traps, many of the same measures used to combat theft and vandalism by people can be employed (**Chapter 10-6**), including the use of **security cases and metal posts** (e.g. **Figs. 10-2 and 10-8**). Even these measures may not stop elephants though. One tactic is to weld sharp metal spikes to the outside of security cases, which has proved effective in one study in Thailand (Grassman *et al.* 2005). Another study in Malaysia protected camera traps from elephants using piles of large logs (Ancrenaz *et al.* 2012). You can also place your camera traps above the reach of animals with poor climbing abilities, but note that detection probabilities for many species will decline the further from the ground you have to place cameras (e.g. Meek *et al.* 2016b). If security cases are not deemed necessary, it may still be necessary to use **padlocks** to stop animals – especially inquisitive monkeys – from opening camera traps (many camera trap models have a padlock loop on the outer casing for this purpose).

It is also important to realise that many animals will be reacting to the sounds and smells emitted by your camera traps (Meek *et al.* 2014b). Using camera traps with **low- or no-glow infrared flash will greatly reduce the disturbance caused to animals** and will result in fewer attacks on your equipment. You can also attempt to hide your cameras, by attempting to camouflage them, and keep disturbance to vegetation at an absolute minimum. You should also minimise the amount of **scent** you leave behind on your camera traps and in the surrounding area. Separate your camera traps from food when transporting them into the field, for example using air-tight bags. Handle your camera traps with clean, dry hands (you can also wear gloves) and do not smoke cigarettes near to camera traps or at sampling locations.

For dealing with ants and termites, odourless insecticide can be applied to the camera trap, and petroleum jelly can be used to create an insect barrier on the tree or post the camera is attached to (ideally, both above and below the camera trap). Note that these substances may alter the behaviour of other species, and this drawback should be weighed against the benefits of reduced damage by insects. Steel wool, which is resistant to the mouthparts of ants and termites, can be used to protect any vulnerable access routes into a camera trap (e.g. around the pressure vent on a Reconyx camera trap). It is also best to avoid deploying a camera trap near to any obvious ant or termite nests.

10-8 Arboreal camera-trapping

Commercial camera traps are designed and tested by manufacturers to work on the ground. However, in forested habitats, a substantial proportion of biodiversity lies in the canopy. Camera trap researchers are increasingly exploring the use of camera traps at height, with promising results. For example, Olson *et al.* (2012) demonstrated the potential of arboreal camera-trapping to survey for the greater bamboo lemur, *Prolemur simus*, in Madagascar. They placed cameras strategically in the sub-canopy at heights of up to 8 m. Gregory *et al.* (2014) went even higher, placing camera traps at 30 m to monitor the use of natural canopy “bridges” across gas pipeline clearings in Peru. Over 6 months, they documented 16 mammal species which were not picked up by ground-based camera traps, as well as a significant range extension for a species of dwarf porcupine, *Coendou ichillus* (Gregory *et al.* 2015). Whitworth *et al.* (2016) compared arboreal trapping to line transects in Peru, finding that cameras were cost-effective for monitoring some species (especially hunted primates and nocturnal species, both of which are hard to detect using line transects) and that placement in the upper canopy (~ 30 m) was more effective than the mid-canopy (~10 m). Also in the Peruvian rainforest, Bowler *et al.* (2016) deployed 42 camera traps (at ~20 m) in a grid-based design, using multi-species occupancy methods to robustly monitor a community of arboreal mammals for the first time.

The two major constraints of arboreal camera-trapping are **misfires** and **canopy accessibility**. Misfires accounted for 98% of images recorded by Gregory *et al.* (2014), primarily due to the movement of warm leaves close to the camera. Any leaves in the detection zone should be removed, as long as it is safe to do so. Accessing the canopy and setting up cameras at height is labour- and time-intensive, requiring 2-10 hrs per tree (Gregory *et al.* 2014; Bowler *et al.* 2016). Moreover, working at height can be highly dangerous and requires extensive training in **safe canopy access techniques**.

For mounting camera traps in the canopy, a dedicated camera mount with a ball head is recommended (Gregory *et al.* 2014; Bowler *et al.* 2016; **Chapter 10-4-2** and **Fig. 10-11**). However, if interference by animals is a problem, mounting camera traps onto sturdy L-shaped brackets may be more effective (Bowler *et al.* 2016; **Fig. 10-11**). Due to the difficulty of making regular camera checks, lithium batteries and large memory cards (e.g. at least 16 GB) are recommended (Gregory *et al.* 2014). Networked camera traps (especially wireless camera traps, such as the Reconyx Microfire cameras) may be particularly effective for arboreal trapping, to enable cameras to be checked from the ground.

Figure 10-11. Arboreal camera trap deployment. Cameras should be fixed near to the trunk of the tree to minimise movement from wind and are most effective if aimed at large branches (**A**). The field of view of the camera trap in A is shown in B. Camera traps can record rare behaviours of species, such as *Aotus nigriceps*, which are difficult to otherwise monitor (**B**). Cameras can be fixed in the canopy using ball head (**C**) or L-bracket (**D**) mounts. Images © Tremaine Gregory (A and B) and © Mark Bowler (C and D).

Analysis methods for arboreal camera-trapping are broadly the same as for ground-based camera-trapping. Care should be taken, however, with any methods that assume random placement. Safe canopy access requires selecting only certain trees of certain species. Sampling designs for arboreal camera-trapping will therefore require additional flexibility in camera trap placement than typically allowed under strict random placement.

In addition, given the heavy equipment involved in canopy access (> 20 kg), and therefore the difficulties associated with transporting equipment between sampling points, it may be more effective to use a **clustered sampling** design (e.g. deploying pairs of camera traps in the same tree, or nearby trees).

10-9 Common problems encountered in different environments and potential solutions

	Relevant environments									
Potential study problem	Tropical forest	Temperate and Boreal forest	Forest canopy	Dense scrub or shrubland	Grassland and savanna	Desert	Polar and high mountain	Agricultural	Urban	Underwater
Theft and vandalism	✓	✓		✓	✓	✓		✓	✓	
Damage from wildlife	✓	✓	✓	✓	✓	✓	✓	✓		✓
Corrosion of electronics due to humidity	✓	✓								
Water ingress	✓	✓	✓	✓	✓		✓	✓		✓
Extremes of temperature		✓	✓	✓	✓	✓	✓	✓	✓	
Difficult access to parts or all of the study area	✓	✓	✓	✓		✓	✓	✓	✓	✓
Dense understorey vegetation or other obstructions in the field of view	✓	✓		✓	✓			✓	✓	
Lack of suitable mounting options in the environment			✓	✓	✓	✓	✓	✓	✓	✓
Lack of a suitable triggering mechanism			✓		✓	✓				✓
Lots of blank images caused by misfires			✓		✓			✓	✓	

Table 10-1. Problems commonly encountered during camera trap studies in each of ten broad environments.

Potential study problem	Potential resolutions
Theft and vandalism	Security case and cable lock; concreted steel post; off-trail sampling locations; covert deployment with camouflage; installing cameras high up in trees; regular checking on camera traps or maintaining a presence in the area; signage in the area and on cameras; inform and engage local communities
Damage from wildlife	Infrared (ideally "no-glow") flash to avoid disturbing animals; sealed and lockable camera casing; reinforced steel case; secure attachment to object (e.g. cable lock or screw-mounted); custom case with spikes; deterrents (e.g. odourless insecticide); avoid leaving strong smells on the cameras (e.g. food or cigarette smoke)
Corrosion of electronics due to humidity	Silica gel inserts; "conformal" coating on circuit board and other electronics; storage in dry conditions (e.g. using a dry cupboard); avoidance of the "condensation effect" (in hot conditions, store at ambient temperature; in cold conditions, place camera trap in a sealed plastic bag and allow to come to room temperature before storage); seasonal deployment, avoiding humid periods of the year
Water ingress	Waterproof case with O-ring seal around any Chapters which can be opened by the user (silicone grease can also be used to make sure the seal is water-tight); make-shift rain covers to place over cameras (e.g. made out of plastic Tupperware or corrugated metal); deployment away from rivers (or well above the high water mark if unavoidable); dry season deployment, avoiding wet season
Extremes of temperature	Using high-end cameras with a wide operating temperature range; deployment preferentially in shady or covered areas; use of appropriate batteries (e.g. Ni-Mh quickly discharge in hot conditions; alkaline batteries perform poorly in cold conditions)
Difficult access to part or all of the study area	Proper budgeting for the additional time and resources needed to reach remote field sites; if study area contains private land, additional work to gain trust and support of local land-owners; stratification of study area into "accessible" and "inaccessible" parts, with all inferences restricted to the former; networked cameras, to monitor when a camera actually needs visiting; solar-powered cameras, to reduce the number of visits required
Dense understorey vegetation or other obstructions in the field of view	Systematically aiming cameras in the direction which is least obstructed at each sampling point; removing obstructions from the environment (e.g. cutting back vegetation directly in front of a camera); allow for some deviation from strict random placement of cameras (e.g. > 10 m); use non-random placement of cameras, combined with appropriate models to account for this; stratify the study area, with inferences restricted to open understorey areas
Lack of suitable mounting options in the environment	Use cut poles, wooden stakes, metal posts or rock cairns to mount cameras; allow for some deviation from strict random placement of cameras (e.g. > 10 m), if nearby mounting options are available in the environment (e.g. isolated trees in grasslands), but beware of biases introduced into the data; use fully non-random placement of cameras, combined with appropriate models to account for this
Lack of a suitable triggering mechanism	Consider active instead of passive infrared triggers; trial other types of trigger which might be effective for your target species (e.g. pressure plates or pixel-detection); modify the thermal properties of the background environment to make passive infrared sensors more effective (e.g. using a cork tile); focus on micro-habitats in your study area which will allow passive infrared sensors to be more effective (e.g. shaded or cooler areas), restricting your inferences to only these micro-habitats
Lots of blank images caused by misfires	Clear/cut vegetation directly in front of the sensor which might trigger the camera if blown by the wind; more frequent checking of cameras, to replenish battery and memory, and to cut back vegetation if necessary; avoid facing camera directly to east or west in open environments (due to misfires caused by the sun); reduce the sensitivity of the trigger, bearing in mind this must either be the same across all cameras, or accounted for during modelling; restrict sampling to periods of the day when misfires are lower (e.g. at night)

Table 10-2. Potential resolutions for each of the common problems encountered in camera trap studies.

Camera traps are being deployed in new environments and in new ways, for example to monitor forest canopy species. This is generating vast amounts of camera trap data around the world. A significant bottleneck has long existed in managing and processing all of this data, but new software tools promise to unblock the flow of information from camera traps into research and conservation.

Image of white-fronted capuchins, *Cebus albifrons*, in the canopy: © Andy Whitworth / Crees Foundation

11 MANAGING AND PROCESSING CAMERA TRAP DATA

HIGHLIGHTS

- The processing of the vast amount of data that camera traps can quickly generate is often the most significant bottleneck in camera trap surveys, and far too much data has historically remained unexploited as a result
- Before a camera trap survey begins in the field, careful thought should be given to how data will be organised and linked together; this includes the camera trap data itself (images and video), information about sampling effort, and any covariate data you will use to explain the patterns in the data
- When managing your data, you should always distinguish between raw data (e.g. camera trap images or data transcribed directly from field notebooks) and derivative data (e.g. data tables you create to use with specific analysis software) and keep them separate
- Dedicated camera trap software will establish a logical system of organising and linking your data for you, and the software options are becoming increasingly sophisticated and user-friendly; however, you will need to invest time to trial the different options and to setup the software, and it may make the underlying data less accessible
- Document everything you do, both in the field and with your data, with appropriate metadata; a standard set of metadata fields to follow already exists (the “Camera Trap Metadata Standard”)
- The steps in downloading data from your camera traps are: create the folder structure on your hard-drive; copy the images from each memory card to separate folders on your hard-drive; backup the images; format the memory cards, and lastly rename all the images with unique names
- In order to turn the raw camera trap image or video data into data for analysis there are four main pathways: 1) manual data entry into a spreadsheet (which should be avoided); 2) cataloguing images by sorting them into separate folders on your hard-drive; 3) cataloguing images by adding keyword tags to them, and 4) using dedicated camera trap software
- Emerging approaches to turn raw camera trap data into data for analysis include citizen science “crowdsourcing” and automated species identification (e.g. using machine learning)
- All data storage mediums have a shelf-life, so it is essential that data is backed up; best-practice is to obey the “rule of three”, i.e. have two on-site copies and one off-site copy of your data
- A wide range of camera trap software is now available, each with strengths and weaknesses; no single piece of software can currently do everything

Modern digital camera traps can quickly churn out thousands of camera trap images or videos, but in no way help the user to make sense of them. A given memory card may contain 10,000 images of moving grass, with just a single photo of a leopard. Another memory card may contain 100´s of images of a baboon troupe passing in front of the camera. Yet another card may contain data from just one week of sampling, before it malfunctioned. How can this cacophony of raw image data be quickly and accurately coded into useful **quantitative data** to act upon?

This step in the camera-trapping process remains a **significant bottleneck** for many researchers and conservationists around the world, especially those in the applied sector with scant resources for laborious manual processing. This has meant that vast amounts of hard-won data have remained unexploited, gathering dust inside computer hard-drives, rather than generating insights about species and guiding the conservation and management of species.

This Chapter deals with the methods used to extract and record the information contained within camera trap images or videos, as well as the most useful ways to catalogue images and video for posterity. This is still a rapidly evolving field, with new software packages regularly appearing (reviewed in **Table 11-1**). However, the broad principles outlined here should remain instructive, irrespective of the exact software packages used.

11-1 Data management considerations for camera-trappers

11-1-1 Establish a logical system of organising and linking your data

A camera trap study will typically have various pieces of raw data which are collected more-or-less separately, but will need to be combined at some point if any sense is to be made of them. In particular, a given study will usually have a minimum of:

- The **camera trap data**, i.e. images or videos
- A table of information about **sampling effort**, i.e. the dates when each sampling point was monitored by a camera trap
- A table of **covariates** and other metadata for each sampling point, such as habitat characteristics

Other pieces of raw data might be a table for keeping track of camera traps (including: model and serial numbers; if they are functioning, and what repairs have been done on them), or anecdotal information on animal sightings.

By establishing a logical system of organising and linking all of the pieces of raw data, you will save lots of time in the long run. An efficient way to achieve this for large datasets is using a **relational database** (e.g. in Microsoft Access or an SQL database). This efficiently breaks large data tables up into smaller sub-tables, to avoid repetition of data. This will force you to think logically about how all of your data is related, and will likely be a necessity for very large projects. However, it may involve significant **set up costs**, and make your data less accessible and harder to understand (humans are very bad at mentally linking up lots of small tables).

For most small- and medium-sized camera trap surveys, the efficiency savings of using a relational database might not be worth the cost of making it less accessible. Instead, an informal kind of relational database might suffice. In this case, you would just maintain a minimum of: 1) a table for **sampling effort**, 2) a table for **covariates** and, 3) after processing your images or video (see **Chapter 11-3**), a **table of information extracted** from them. Depending on the analysis, data can then flexibly be linked together in the correct format, using spreadsheet software (e.g. Microsoft Excel) or a programming language (e.g. R, Python or MATLAB).

In each table, each row would represent a unique record, and would be given a unique "key" (sometimes called a "primary key") to identify it. So the sampling effort table might, for example, look like this:

Deployment ID	Sampling point name	Camera on (date & time)	Camera off (date & time)	Camera trap used (name or serial no.)
1	PlotA-1	31-01-2017 09:30	31-03-2017 16:30	Camera1
2	PlotA-2	01-04-2017 14:00	05-07-2017 15:30	Camera3
3	PlotA-1	01-05-2017 10:00	30-06-2017 11:30	Camera2

In this case the "key" column is the deployment identification number (as indicated by the key icon). If you only ever sample each sampling point once, then the sampling point name could also be the key, but using a deployment identification number allows for cases when points are repeatedly sampled.

The table of covariates might look like this:

Sampling point name	GPS Latitude (EPSG: 4326)	GPS Longitude (EPSG: 4326)	Elevation (m)	Canopy cover (%)
PlotA-1	20.51222	-75.4164	560	75
PlotA-2	20.52417	-75.4706C5	720	80
PlotB-1	20.48639	-75.7892	650	25

The name of each sampling point will function as the key here, since these are unique and associated with a single row of covariates. If points were re-measured for some reason (perhaps to account for changing canopy cover across different years of sampling), then an ID column would have to be created, as for the sampling effort table above. GPS coordinates here are given in the standard World Geodetic System of 1984 (WGS 1984), which is the default setting on most GPS units. If you use any other coordinate reference system, such as a local system for your area of interest, you should note down its exact name and ideally attach the EPSG code to the column names (as shown here; you can find EPSG codes on www.spatialreference.org).

Now, each deployment ID in the first table can be linked, when required, to the relevant covariates by using the sampling point name in the second table. Finally, we can also link these tables to the actual information extracted from the camera trap data, again using the sampling point names. This last table, containing the information from the images or videos, could look like this:

Image filename	Sampling point name	Species	Group size	Age class
PlotA-1_20170403_102903.jpg	PlotA-1	Mammal species 1	3	Adult
PlotA-1_20170407_114931.jpg	PlotA-1	Bird species 1	1	Sub-adult
PlotA-1_20170407_210212.jpg	PlotA-1	Mammal species 2	1	Adult

Here the image filenames are the key, and they should ideally be unique (see **Chapter 11-2**). If they are not unique (perhaps they are in different sub-folders, to allow duplicates), you can include an image ID column in this table to function as the key, but you might in this case also want to include the file directory paths in another column, to help you locate a given file if required. Note, this table could have been manually or automatically created, and methods for doing this are discussed in **Chapter 11-3**.

11-1-2 Distinguish between raw data and derivative data and keep them separate

You should **never edit raw data** directly. Raw data should be directly taken from the camera traps, or directly recorded from notebooks, and then kept for posterity. If you are carrying out data cleaning, or combining raw data into a format more suitable for analysis (e.g. with a specific software program), you should create new files and clearly label them as such. We call these **derivative data**, as opposed to raw data. For any derivative data you create, it is best-practice to make clear notes on how exactly they were created (note, if they have been created automatically using code, such as in R or MATLAB, then the code can function as your notes!).

The most important derivative datasets you will create in a camera trap study will be the tables containing information that has been extracted from the raw camera trap data (**Chapter 11-3**). Most often this will be the times, dates and locations of species seen in the images, as well as any accessory information (such as age class, sex, individual identifications, behaviour etc.). However, it is important to be clear that this is derivative data, and the exact process by which it was created from the raw camera trap data should be documented.

11-1-4 Should I use dedicated camera trap software to manage my data?

If you use specifically-designed camera trap software (see **Table 11-1** for available options), it will do most of the hard thinking for you, including forcing you to organise and link your data efficiently (usually using a relational database in the background), and keeping any derivative data separated from your raw data. However, the drawbacks of using camera trap software are:

- The **set up costs** of having to convert your own raw data tables into the format accepted by the software
- It may make it **harder to access and understand** the underlying data
- The databases are relatively **inflexible**, meaning that complex or unusual study designs might not easily be accommodated
- It may make it **harder for multiple people** to work on a database or to collaborate with others if they are using a different software platform

Importantly, no single software package has emerged as a favourite amongst camera-trappers, and lots of very different solutions to the problem of camera trap data management are currently being trialled (**Table 11-1**). For any given camera trap project, and especially those that are making plans for long-term data collection and storage, this makes it difficult to decide which software package to commit to. Many large camera trap projects, such as eMammal and the TEAM Network, have ended up designing their own systems from scratch.

11-1-3 Document everything you do, all the time, with metadata

We over-estimate our ability to remember minute details and events, and this fact is often laid bare to anyone who has revisited their own poorly-documented data after a long, or even a short, break. Things you felt certain you´d remember – which sampling point had the camera knocked over by an elephant, which memory card you spilt hot coffee over, or how exactly you measured tree height – will be a distant memory all too quickly. Whether you are in the field, in the lab, or on the computer, it is vitally important to **clearly document everything you do**. This not only makes your own work easier, but makes it easier for others to build upon what you´ve started at a later date, and makes it easier for you to share your data and collaborate.

The Ecological Metadata Language (EML) provides a best-practice framework for documenting ecological studies, and may help you decide what information about your study is critically important to record (Fegraus *et al.* 2005). A consortium of some of the biggest camera-trapping institutions have also agreed upon an open data standard specifically for camera trap data - the Camera Trap Metadata Standard (CTMS; Forrester *et al.* 2016). This has been designed to enable greater standardisation and sharing of camera trap data.

Common problems in camera trap surveys include: poorly-documented methods (how high off the ground did you set your camera traps again?), using undefined acronyms or coding systems in data tables, missing measurement units in data tables, and the “ghost camera trap”. You have a ghost camera trap when you suddenly find a folder of camera trap images with no location information! Without location information, this renders the data almost useless. This all-too-common situation can be prevented by doing a number of different things:

Further reading: Borer *et al.* (2009) provide an excellent and simple set of guidelines for effective data management in ecological studies; Hart *et al.* (2016) provide technical advice for managing and sharing large ecological datasets, and Scotson *et al.* 2017 provide 9 clear recommendations specifically for managing and sharing camera trap data. Finally, Meek *et al.* (2014c) discuss the many ways in which camera trap studies can vary, and the metadata which should be reported in any publications using camera trap data.

1. After setting up each camera trap in the field, trigger it to take a photo of a dry-wipe whiteboard showing the current date, time and location
2. Make use of any image labelling function on your camera trap to permanently stamp images with the location name (this is sometimes called a “user label” or “camera name”)
3. Download data from memory cards into separate folders and immediately rename the folders with the camera location names (the sooner you do this after coming back from the field the better!)
4. Use image editing software to digitally tag images with the location name (see **Chapter 11-3** for more information on tagging images)

11-2 From the field to the hard-disk

Now imagine you´ve just collected your first camera trap in from the field, with a memory card stuffed full of exciting images. What are you going to do next?

The first thing to do is to create the **folder hierarchy** on your hard-drive that will receive the files. A suggested hierarchy is: Project → Study site → Sampling point. Give your folders useful names which will help you to locate them in space, and avoid spaces and special characters. If you are resurveying sampling points, for example in a long-term monitoring project, then you may have an additional bottom layer in the hierarchy that specifies the start date, e.g. Sampling point → Deployment20170131 (for a start date of 31st January 2017). If you have paired cameras at a sampling point, these can also be added into the hierarchy at a lower level still, e.g. Deployment20170131 → Camera1. You may also have additional levels between a study site and a sampling point if your points are in some way clustered, for example into sampling blocks.

Some camera-trappers prefer to organise their folders according to discrete camera surveys, i.e. all the data obtained from a group of cameras that were deployed together (e.g. Project → 2017WinterSurvey). This may also be acceptable in your case, but will not make sense in a long-term monitoring project that does not have clear breaks in sampling.

The absolute minimum requirement at this stage is that images from each memory card are kept separate on your hard-drive and that the folders are named after the sampling point (the most important information). The names should exactly match those recorded in your sampling effort and covariate tables (**Chapter 11-1-1**). The R package “camtrapR” (**Table 11-1**) can automatically create folders on your hard-drive according to a data table, which may be faster and less error-prone than creating them manually.

The next step is to **copy the images** over from each of the memory cards (copying is usually safer than using the "cut" function in your file explorer). You can also immediately copy the images to an external hard-drive as a **backup** of the raw data, and-or upload them to a cloud storage platform (**Chapter 11-4**). Once this is done, you can **format the memory card**, which clears the memory entirely and maximises the number of images it will be able to record when it is next used (note, you will not be able to recover any files from the memory card once it is formatted, hence why the backups are so important).

The final step is to rename all the images on your hard-drive with a **unique file name**. This helps reduce ambiguities and conflicts in your data later down the line (e.g. in your data table of information extracted from the images) and serves as a backup of the image's metadata. Dedicated renaming software can be used to do this most effectively (e.g. ReNamer, ExifPro, or ExifTool), but some of the camera trap software options can also do renaming (e.g. camtrapR and MapView Professional).

To recap, the steps in extracting data from camera traps are:

1. Create the **folder structure** on your hard-drive
2. **Copy** the images from each memory card to separate folders on your hard-drive
3. **Backup** the images on an external hard-drive and-or upload to the cloud
4. **Format** the memory cards
5. **Rename** all the images with unique names

11-3 Extracting information from camera trap data

The next step is to turn all of the image or video pixel data into useful information, which can then be used to fit statistical models and test hypotheses (**Chapter 12**). There are four main pathways for doing this, all of which require substantial time commitments in manually reviewing the data. In addition to that, there are some emerging approaches utilising citizen science and-or machine learning tools.

11-3-1 Manual data entry into a spreadsheet (Option 1)

Manual data entry of information contained in camera trap images or videos is the simplest, but also the most laborious and error-prone method. It involves sequentially reviewing the images or videos and then typing the information (e.g. location, date, time, and species) into a **spreadsheet**. This has traditionally been a common way of extracting information from camera trap images and videos, but better methods now exist (Options 2 and 3) and it **should be avoided** as much as possible. As well as being slow and liable to errors, this method also severs the link to the original camera trap data. One way to circumvent this is to paste the full file path into the spreadsheet as well (although if the file is moved or renamed this link will break). In addition, it is possible for subjective decisions made by the user to creep into the data entry process, unless the methods are very precisely defined in advance. In particular, a decision must be made whether every image or video will be represented by a row in the data table, or whether rows will consist of "independent" detections (e.g. detections separated by more than 30 minutes or clearly a different individual). Only entering data on detections will be much faster, but discards more information from the images or videos, and it may be even more likely that undocumented and subjective decisions by the user creep into the process.

Note, manual data entry may be the only feasible approach for extracting information from film camera traps, although optical character recognition may help to some degree (as available, for example, in Camera Trap Manager; see **Table 11-1)**. Film camera traps, being limited to the number of images on a film roll, produce far fewer images than modern digital cameras, which makes manual data entry a more realistic proposition.

11-3-2 Image cataloguing using drag-and-drop (Option 2)

Perhaps the first thought when faced with a large number of uncatalogued images or videos is to digitally **sort them into separate folders** on your hard-drive. This "drag-and-drop" cataloguing, if done carefully and systematically, is a simple method of extracting information from a moderately-large dataset. However, it is likely to be **error-prone**, and is relatively **inflexible** in terms of the structure and type of information than can be extracted from the camera trap data.

The idea is to place images (or videos) in a hierarchy of folders which reflect the spatial locations of camera traps (as in **Chapter 11-2**) and, more importantly, the species and the number of individuals present in the images (or videos). For example, an image of two leopards at a sampling point called "PlotA-1" would be placed into the folder structure: Project → Study site → PlotA-1 → Leopard → 02. In practice, the method typically involves flipping between a program for viewing the images (or videos) and a file explorer for moving the images. The R package "camtrapR" (**Table 11-1**) can be used to automatically create a hierarchy of folders based on a data table of sampling locations and a species list. After moving images to their relevant folders, another function is available to automatically delete all empty species folders.

This "drag-and-drop" approach is compatible with a basic Fortran program written by Jim Sanderson, as well as camtrapR (see **Table 11-1** for further details). The images do not have to be inspected again, and these two methods create a csv file of images with associated metadata by processing the file paths for each image. See Harris *et al.* (2010) and Niedballa (2017) for more specific details on the approach.

11-3-3 Image tagging using photo-editing software (Option 3)

A rapid and flexible approach to extracting information from camera trap images is to use widely-available photo-editing software (e.g. Adobe Lightroom or digiKam). This involves adding relevant information, such as the location and species, to the metadata **stored within the image files** themselves. Each piece of information constitutes a "tag", and they are added to the **"keywords" field** of the metadata. This is typically done in photo-editing software by typing the information into a text box, or using tick-boxes. These keyword tags are then permanently associated with the images, even if they are moved, shared with someone else, renamed or viewed in another photo-editing program. The information in the keywords field should be coded in a highly standardised way (e.g. species names should have a consistent format and case) and, ideally, hierarchically structured (e.g. "Species: Mammal species 1; Location: PlotA-1"). A suggested structure, which can be used with the R package "camtrapR", is given by Niedballa (2017).

Once the metadata has been added to the images, a **data table can then be made automatically** (e.g. using ExifTool, ExifPro or camtrapR to export to a csv file). This is a highly repeatable and verifiable process, and also has the benefit of extracting all the metadata present in the image. Depending on the camera trap model, this extra metadata may include the camera settings used (e.g. whether the flash fired, exposure settings, etc.), camera serial number, and data from any sensors (e.g. temperature, pressure, etc.). Exactly how much of the image metadata is successfully extracted depends on how much of the metadata is locked up by the camera trap manufacturer into the proprietary "MakerNotes" field, and the software that is used (e.g. ExifTool is particularly powerful and can decode the MakerNotes field for some manufacturers).

Unfortunately, **videos do not have a highly standardised metadata format**, like images do. For images, camera traps almost always record metadata (such as the date and time it was taken, and any camera settings etc.) in a specific format, namely the Exchangeable Image File Format (EXIF). Some video formats, such as AVI and

MOV, support EXIF, but your camera trap may not record information in this format (or at all). You can check what metadata is available in your videos using a metadata viewer (ExifTool is particularly good at extracting as much as possible from media). In particular, if there is no date and time available, then you will need to manually record that information when viewing videos yourself.

For tagging videos with keywords (and possibly also dates and times), you will need to use photo-editing software capable of doing it (e.g. Adobe Lightroom or digiKam). Whilst the EXIF keyword field is available for some video formats, it is probably best to use another metadata format, namely the Extensible Metadata Platform (XMP). Like EXIF, XMP also contains a keyword field, but it is available in a much wider range of video formats. Recent efforts to standardise metadata for videos are also adopting XMP (e.g. the International Press Telecommunications Council).

11-3-4 Image cataloguing using dedicated camera trap software (Option 4)

With ongoing and rapid developments in camera trap software (see **Table 11-1**), using a dedicated program is **increasingly becoming the most efficient way** to extract information from raw camera trap data. This involves reviewing and cataloguing the images or videos directly within the software, for example by selecting any species present in an image or video from a custom drop-down box or tick-box.

The various software options available **differ greatly in their approaches** (**Table 11-1**) and you may need to test various options before deciding which one satisfies your requirements and most efficiently fits into your workflow. One thing to note is that they differ in how they record the information extracted from the images: some only record the information in a database (e.g. Camera Base), whilst others also edit the metadata of the underlying images (e.g. Aardwolf). This is important if you will be moving or renaming images after processing them (which is not generally recommended), since the link between the database and the images will likely break in this case, and it will be useful therefore to have a backup of the metadata inside the files themselves. Equally, it will be useful to have the metadata recorded inside the files if there are any plans to view or search for images in different software environments (e.g. photo-editing software or a file explorer).

As noted above (**Chapter 11-3-3**), **video cataloguing is problematic** because of the lack of standardised metadata. As a result, most of the dedicated camera trap software options do not currently support video or, if they do, there may be problems with the implementation. For example, it is possible to infer the date and time the video was taken from the "date modified" or "date created" metadata, but this is highly liable to modification (e.g. by file browsers or other software). Other options are to use optical character recognition (proposed for Camelot) or automatic harvesting and importation of file creation dates directly from memory cards (proposed for Agouti). For now, the safest option is manual cataloguing of the dates and times of videos.

Dedicated camera trap software may offer some advantages over general photo-editing software when cataloguing images, for example by automatically clustering together images from the same animal capture event or from opposing camera traps (as used in a paired design). Some programs (e.g. TRAPPER, Wild.ID) pull in species lists from online taxonomies to ensure standardisation across images and across projects. In addition, some programs ensure that data is recorded and packaged in a way that is consistent with metadata standards (see **Chapter 11-1-3**), such as EML (e.g. TRAPPER) or the Camera Trap Metadata Standard (e.g. Agouti, eMammal and Wild.ID). However, camera trap software may not be as fast, robust or user-friendly as general photo-editing software.

11-3-5 Emerging approaches to processing camera trap data

A number of large-scale camera trap projects (e.g. eMammal, Mammal Web, and various projects on Zooniverse.org) are using **citizen scientists**, both to deploy camera traps in the field and catalogue camera trap images. For example, the Candid Critters eMammal project hopes to sample tens of thousands of locations across the whole state of North Carolina in just a few years by harnessing the power of citizen scientists. This could make it the biggest camera trap study to date. Members of the public can use their own cameras, or loan one from a public library. They receive some online training, and can then start collecting data on their own. The system makes use of the eMammal software and cloud architecture to help citizen scientists effectively manage and catalogue their data, and then submit it for expert review by professional scientists (McShea *et al.* 2016). A similar system – where citizen scientists were supplied with in-person training and camera traps – was previously trialled with great success across six states in the US (Kays *et al.* 2015, 2017).

Candid Critters eMammal project
www.nccandidcritters.org

Snapshot Serengeti project
www.snapshotserengeti.org

The Snapshot Serengeti project is the best example to date of the collective power of citizen scientists for cataloguing camera trap data. This project uses members of the public to **"crowdsource" species identifications** in images, using algorithms which are also capable of flagging up images which need expert review (e.g. those for which users disagree). During the validation phase (2010 to 2013), the platform received more than 10 million identifications, and crowdsourced identifications achieved more than 96% accuracy when compared to expert identifications (Swanson *et al.* 2016). It has recently become possible for any camera-trapper to set up a project on the Zooniverse platform used by Snapshot Serengeti (costs are incurred for large projects requiring significant cloud data storage), and templates already exist for species identification in camera trap images. More unusual tasks, such as transcribing behaviour or tracking motion, will require specialist input from Zooniverse (with attendant costs). To achieve the success of Snapshot Serengeti requires a significant investment of time to setup and manage the crowdsourcing (for example, to recruit volunteers and then keep them engaged, and to validate identifications). This approach will likely be best suited to large camera trap projects with a considerable bottleneck in the image cataloguing phase.

Humans are exceptionally good at visually classifying objects, but computers are fast catching up. There are two main tasks which computers will increasingly be employed in: identification of individuals from their pelage patterns (for capture-recapture studies), and identification of species. Software for **computer-assisted identification of individuals** already exists (e.g. see "Extract Compare" and "Wild-ID" in **Table 11-1**), and has been successfully employed in a small number of camera trap studies to date (e.g. Hiby *et al.* 2009; Jiang *et al.* 2015). Automatic identification of individuals will be most useful in studies involving lots of different individuals, or if the pelage patterns of the focal species are particularly complicated.

Automatic identification of species is the most widely useful camera-trapping task that could be achieved using computers. A number of research groups are now actively working on methods to achieve this (e.g. Yu *et al.* 2013; Chen *et al.* 2014; Gomez *et al.* 2016). Identifying species in camera trap images is a very special case of object recognition in images, largely because it is so challenging and the "reference" datasets for training the algorithms can be relatively small (especially for rare species, often of most interest from a conservation point-of-view). For example, lighting conditions can vary hugely, images are a mixture of colour and black-and-white (under infrared flash), different camera traps produce images with different characteristics, and animals are highly deformable objects (e.g. the shape of a sitting cat is very different to that of a running cat). Yu *et al.* (2013) used a type of edge- and pattern-matching method, achieving an average of 82% accuracy for a range of species from Panama (in a rainforest environment) and the Netherlands (in heathland). However, this accuracy was achieved only after manually cropping images around animals present in the images, which is a very laborious process. Gomez *et al.* (2016) used state-of-the-art machine learning methods on samples of images (1000 per species) from Snapshot Serengeti (a savanna environment), achieving an average of 50-70% accuracy across different algorithms. This increased to 70-90% if the images were manually cropped, with 18 of 26 species being classified with > 90% accuracy using the best-performing algorithm. Methods to automatically extract animals from images, which will greatly assist automatic species identification, are in development (McShea *et al.* 2016). In addition, greater availability of open-access camera trap datasets (e.g. Swanson *et al.* 2015) will allow for faster developments in the field of automatic species identification. In the future, these algorithms will become an essential part of the camera-trapping process, seamlessly integrated into camera trap software, as anticipated by eMammal and TRAPPER (Bubnicki *et al.* 2016; McShea *et al.* 2016), and possibly even into camera traps themselves.

11-4 Backing up and sharing camera trap data

Everyone will experience a complete failure of a storage medium at some point, and Murphy's Law says that it will always happen at the most catastrophic moment possible. Best-practice is to obey the **"rule of three"**: ideally you should have **two on-site copies** of all of your data (one on your main computer's hard-drive, one on an external hard-drive) and **one copy off-site** (e.g. on another hard-drive or on a cloud data storage platform such as Dropbox or Amazon S3). Back-ups should be regularly inspected and, ideally, tested to see if they can perfectly function as a replacement for the live dataset.

Sharing camera trap datasets can be challenging, due to their large size. Fast internet and cloud data storage platforms have recently made it a realistic proposition for all camera-trappers. Camera trap software can help to properly package the data and make sure it is properly documented with all the necessary metadata (e.g. Agouti, eMammal, TRAPPER and Wild.ID). Alternatively, other software for managing metadata for ecological datasets can be used to make sure all the necessary information is provided (e.g. Morpho). Available repositories for sharing camera trap data include general cloud data storage platforms (such as Dropbox and Amazon S3), as well those linked to camera trap software (e.g. Agouti, eMammal and Wild.ID). The eMammal and Agouti platforms use servers located in museums (in the US and Europe, respectively), storing the data in perpetuity alongside their physical specimen collections. Athreya *et al.* (2014) also provide guidelines for specifically sharing camera trap data on the Global Biodiversity Information Facility (GBIF) platform.

When sharing datasets, any **images of people must be treated with due care**. Although in most countries it is not illegal to collect and share images of people on public or private land, it is probably unethical and unnecessarily intrusive to do so. Images of people should be removed from the dataset, or appropriately anonymised by masking or blurring faces. Images of illegal activity should be treated with an extra level of security, and not shared at all. These images should instead be submitted to the appropriate authorities.

Care must be taken if imagery from camera traps is to be made public, particularly if it includes the spatial locations of **species which are threatened by hunting and collection** (e.g. tigers and other big cats, rhinos, and pangolins). If you are unsure about which species these are, then a good starting point is the list of species on Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). As for images of humans, these images should be removed from the shared dataset, or the spatial locations appropriately "generalized" to ensure they are not used by poachers or collectors.

11-5 Software for camera-trappers

Software	Image cataloguing	Database management	Analysis	Videos	Multiple users	Description*	Years active	References	Website
Google Picasa	Yes	No	No	Yes	No	Not specifically for camera trap data. Photo editing software, with ability to quickly tag images with metadata; may cause loss of metadata in proprietary fields (i.e. in the MakerNotes). Mac version available. Google withdrew support in 2016.	2002 - 2016		Discontinued by Google but available from other websites
digiKam	Yes	No	No	Yes	No	Not specifically for camera trap data. Photo editing software, with ability to quickly tag images with metadata; advanced image search capabilities. Mac and Linux versions available.	2006 - current		www.digikam.org
Adobe Lightroom	Yes	No	No	Yes	No	Not specifically for camera trap data. Photo editing software, with ability to quickly tag images with metadata; advanced image search capabilities. Mac version available. Not free-to-use.	2006 - current		www.adobe.com/products/photoshop-lightroom.html
Camera Base	Yes	Yes	Yes	Yes	No	A customised Microsoft Access database. Particularly useful for capture-recapture surveys; includes automatic matching of paired cameras and can produce density estimates using conventional capture-recapture models. Requires somewhat laborious manual data entry. Can export files suitable for external analysis (e.g. in Presence, DENSITY, EstimateS). Useful for small- and medium-sized surveys (may be slow or crash for large numbers of images, i.e. > 100,000).	2007 - current		www.atrium-biodiversity.org/tools/camerabase
Extract Compare	Yes	No	No	No	No	This simple software tool is not a general tool to help with cataloguing images, and is used just for computer-assisted identification of individuals in images. Specific versions of the tool exist depending on the species of interest (e.g. cheetah, tiger, leopard, lynx, and zebra). It can also rotate and flatten Chapters of an animal's pelage in a camera trap image, to aid with manual identification of an individual.	2009 - 2013	Hiby *et al.* (2009)	conservationresearch.org.uk/Home/ExtractCompare

Software	Image cataloguing	Database management	Analysis	Videos	Multiple users	Description*	Years active	References	Website
"Jim Sanderson scripts"	No	No	Yes	Yes	No	A Fortran program for analysing a table of camera trap data and producing standard outputs (e.g. species accumulation curves, activity patterns and detection rates). Also creates detection/non-detection matrices suitable for analysis in Presence. If images/videos are stored in a specific folder structure, a separate Fortran program can also automatically create the table of camera trap data in the format necessary for the analysis program.	2010	Harris *et al*. (2010)	esapubs.org/archive/bulletin/B091/002/default.htm
MapView Professional	Yes	No	No	No	No	Reconyx proprietary software, but can read images from many other camera traps too. Useful image tagging and advanced search tools. Renames images with unique filenames. Allows export of image metadata to a csv file (for analysis in other software).	2010		www.reconyx.com
Timelapse	Yes	No	No	Yes	No	A tool for quickly cataloguing a large number of images and, if necessary, counting objects in those images by clicking on them. Customisable interface for tagging images (e.g. with user-defined text boxes, dropdown boxes or tick boxes). Includes tools for automatically flagging up corrupted images and for identifying pixel changes across images (which might indicate the presence of an animal). Can export metadata to a csv for analysis in other software.	2011 - current	Greenberg & Godin (2015)	saul.cpsc.ucalgary.ca/timelapse/pmwiki.php?n=Main.HomePage
Wild-ID	Yes	No	No	No	No	This is not a general tool to help with cataloguing images, and is used just for computer-assisted identification of individuals in images. The general feature-matching algorithm this software uses could be useful for a wide range of species with individually-identifiable pelages. It may not be as effective as Extract Compare for comparing images of animals taken at different angles or with different postures.	2011 - current	Bolger *et al*. (2012)	dartmouth.edu/faculty-directory/douglas-thomas-bolger
WWF-Malaysia Tiger Database	Yes	Yes	Yes	No	No	A customised Microsoft Access database. Created for surveys of tiger and clouded leopard, but useful more generally. Can output standard results (e.g. detection rates, activity patterns) and files suitable for further analysis in Presence and CAPTURE.	2012		rimbaresearch.org/2012/01/05/toolbox_update_5/#more-1160

Software	Image cataloguing	Database management	Analysis	Videos	Multiple users	Description*	Years active	References	Website
Aardwolf	Yes	Yes	No	No	Yes	Designed to handle large numbers of images (> 100,000). Contains an underlying SQL database and can export a csv file for analysis in other software. New version (v. 2) runs through a web-browser. Cross-platform (Windows, Mac and Linux).	2013 - current	Krishnappa & Turner (2014)	sourceforge.net/projects/aardwolf github.com/yathin/aardwolf2
Camera Trap Manager	Yes	Yes	No	No	No	Incorporates some GIS capabilities (e.g. for image searching by location). Can also use optical character recognition to extract extra information from image headers/footers (e.g. temperature) which may not be in the metadata. Provides rudimentary analysis (e.g. species counts) and output of metadata to csv and shapefile formats.	2013 - 2015	Zaragozí *et al*. (2015)	github.com/benizar/cameratrapmanager
Colorado Parks & Wildlife (CPW) Photo Warehouse	Yes	Yes	No	No	Yes	A customised Microsoft Access database. User-friendly and simple. Specifically designed to accommodate multiple users (> 1 person identifying, plus a "reviewer"). Can export files for analysis in external software (e.g. MARK, Presence and R). Useful for small- and medium-sized surveys (< 100,000 images). Absolute upper limit of ~1 million images.	2014 - current	Ivan & Newkirk (2015)	cpw.state.co.us/learn/Pages/ResearchMammalsSoftware.aspx
Agouti	Yes	Yes	No	Yes	Yes	Web-based application to aid collaborative cataloguing of large numbers of images. Images are uploaded to the cloud, and then catalogued by multiple users. Can export a csv file for analysis in other software. Not freely-available to download, but authors are willing to share with collaborators.	2015 - current		cameratraplab.org/agouti wu.cameratrapping.net/index.php
eMammal	Yes	Yes	Yes	No	Yes	Comprehensive system for managing and collaboratively cataloguing images, including a desktop program (for inputting images and cataloguing them) and cloud architecture (for expert review of images, basic analysis and long-term storage). Not freely-available to download, with a one-off fee for access and setup, and ongoing charges for cloud data storage (dependent on how much space is required).	2015 - current	McShea *et al*. (2016)	emammal.si.edu

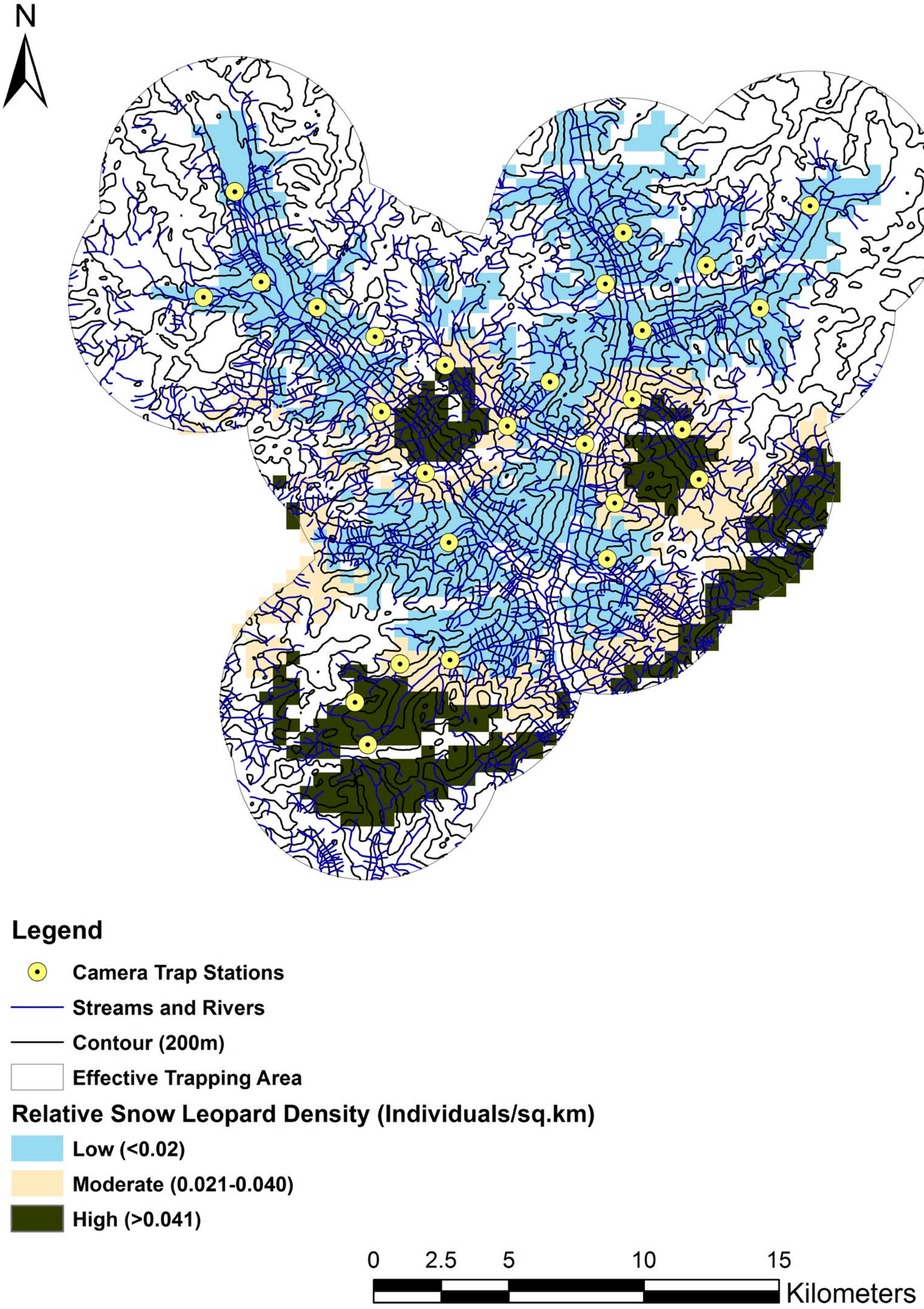
Software	Image cataloguing	Database management	Analysis	Videos	Multiple users	Description*	Years active	References	Website
camtrapR	No	Yes	Yes	No	No	R package which is highly flexible and extensible, but requires proficiency in the R language. Can rename images and adjust date and time. Does not offer any image cataloguing tools (must be done externally). Can create summary tables, maps, and files for occupancy and capture-recapture analysis. Cross-platform (Windows, Mac and Linux).	2015 - current	Niedballa *et al*. (2016)	cran.r-project.org/web/packages/camtrapR/
TRAPPER	Yes	Yes	No	Yes	Yes	Web-based application for managing and collaboratively cataloguing images and videos. Supports map-based display and searching of data. Allows for annotation of videos (e.g. for behavioural studies). Contains an underlying SQL database and can export a csv for analysis. R/Python code examples are provided for analysing outputs. Cross-platform (Windows, Mac and Linux).	2015 - current	Bubnicki *et al*. (2016)	bitbucket.org/trapper-project/trapper-project
Wild.ID	Yes	Yes	No	No	No	Open-source counterpart to DeskTeam, the software used internally by the TEAM Network. Implements a rigid and (relatively) error-proof system of managing a camera trap survey, which has been thoroughly tested at TEAM sites over many years. Data can be easily formatted for uploading to the Wildlife Insights website, for sharing and analysis (e.g. occupancy). Mac version available.	2015 - current		github.com/ConservationInternational/Wild.ID
Snoopy	Yes	Yes	No	Yes	No	Particularly useful for capture-recapture surveys. Includes automatic matching of paired cameras. Contains an underlying SQL database and can export a csv file for analysis in other software. Mac and Linux versions available.	2015 - current	Smedley & Terdal (2014)	www.tulsasoftdb.com/snoopy
SpeedyMouse	Yes	No	No	No	No	A simple program for rapidly cataloguing images using keyboard shortcuts. Particularly useful for quick results from a relatively small number of images. Can export a csv file containing image metadata for analysis in other software.	2016		www.researchgate.net/publication/289202434_SpeedyMouse_22_for_the_analysis_of_camera_trap_images

Software	Image cataloguing	Database management	Analysis	Videos	Multiple users	Description*	Years active	References	Website
Camelot	Yes	Yes	Yes	No	Yes	Desktop application for efficient management and cataloguing of large numbers of images (tested with up to 2 million). Remote users can access a Camelot session over a network for collaborative work. Can export summary reports, with detection rates of species, and a csv file for full analysis in external software (e.g. camtrapR or Presence). Mac and Linux versions available.	2016 - current		gitlab.com/camelot-project/camelot camelot-project.readthedocs.io/en/latest
ViXeN	Yes	No	No	Yes	No	A simple and fast tool for cataloguing images and videos (as well as other media) using a web browser. Advanced search tools. Can export a csv file containing metadata associated with each media file. Mac and Linux versions available.	2016 - current		github.com/prabhuramachandran/vixen

*Except where noted, programs work only on Windows and are free-to-use.

Table 11-1. Software available to assist with cataloguing and managing camera trap images and videos.

Conservation has very much entered the quantitative age. Camera traps, in combination with new statistical models, are improving our understanding of human impacts on wildlife, and enabling more effective management of wildlife populations.



Snow leopard, *Panthera uncia*, density map from camera-trapping in Wangchuck Centennial National Park, Bhutan: © Rinjan Shrestha

12 UNCOVERING PATTERN AND PROCESS USING CAMERA TRAP DATA

HIGHLIGHTS

- Assuming that a study has been well designed and executed, it is possible for the analysis to be relatively quick and simple
- A wide range of software is available for analysing ecological data, some of which may require some level of programming
- Some of the dedicated camera trap software options are also capable of carrying out basic analyses

Methods for the analysis of camera trap data, as well as the reporting and publication of the results, are beyond the scope of these guidelines. However, assuming best-practice has been followed in terms of survey design (**Chapter 7**) and data management (**Chapter 11**), and that any assumptions of the chosen modelling approaches have been satisfied, the analysis may be a relatively pain-free process.

There are many software options for analysis and, unlike for camera trap data management, these are mostly well-established programs which are widely used by ecologists. For example, Presence and MARK both have thousands of users around the world, and there is an active community of people willing to offer guidance and problem-solving help (e.g. see the forum at www.phidot.org).

For cutting-edge, or otherwise non-standard, analyses (e.g. modelling with random effects, or fitting bespoke hierarchical models) it **may be necessary to use programming languages**, such as R, MATLAB or BUGS. R and MATLAB can be used for a wide range of specialised tasks, but can also be used as statistical calculators and for writing your own mini programs (e.g. resampling your data or simulating new data). BUGS (Bayesian inference Using Gibbs Sampling) is a language used to specify models for Bayesian analysis. It is a relatively inflexible language, and variants of it are implemented in WinBUGS (a standalone piece of Windows software with a graphical user interface) and JAGS (which is usually run from within R and is cross-platform).

Even if you are doing relatively straightforward analyses (e.g. using simple capture-recapture or occupancy models), doing it with a programming language has a number of advantages. Importantly, it makes your work more **repeatable** and **replicable** than if it is done using a lot of mouse-clicking. The code effectively functions as metadata for the analyses you have done, showing all the steps along the way. This makes it easier for you to resume an analysis after a break, and makes it easier to share your analyses with others. R also has a very **wide range of packages available** for analysis (those in **Table 12-1** are only a small selection) – it can do pretty much anything you can dream up. If there is no expertise in R in your team, it may be worth investing the time to learn to use R, or collaborate with someone who is already proficient.

Some of the software options for camera trap data management are also capable of carrying out basic analyses, or at least capable of exporting files which are suitable for analysis programs (see **Table 11-1**). There is a trend towards closer integration between dedicated camera trap software and dedicated analysis software (e.g. Camelot and R, via the camtrapR package), and this will likely continue to be enhanced into the future.

12-1: Software for analysing data

Software	Type of analysis	Description*	Years active	Helpful references	Website
EstimateS	Species richness and diversity	Dedicated software for estimating diversity, using asymptotic or rarefaction methods. Mac version available.	1997 - current	Gotelli & Colwell (2010)	viceroy.eeb.uconn.edu/estimates
"vegan" package in R	Species richness and diversity	Conducts diversity analyses, similar to EstimateS, as well as multivariate statistics. Cross-platform (Windows, Mac and Linux).	2001 - current		cran.r-project.org/package=vegan
Presence	Occupancy	Relatively simple, but comprehensive, software dedicated to occupancy estimation. Linux version available. Can also be used for occupancy-based species richness estimation.	2004 - current	MacKenzie *et al*. (2006)	www.mbr-pwrc.usgs.gov/ software/presence.html www.phidot.org (for help forum)
"RPresence" package in R	Occupancy	The R counterpart to Presence. Cross-platform (Windows, Mac and Linux).	2016 - current		www.mbr-pwrc.usgs.gov/software/presence.html
"unmarked" package in R	Occupancy	Implements a wide variety of occupancy and count-based abundance models (the latter are mostly not appropriate for camera-trapping). Actively being developed and supported by a community of users. Cross-platform (Windows, Mac and Linux).	2010 - current		cran.r-project.org/package=unmarked groups.google.com/forum/#!forum/unmarked (for help forum)
CAPTURE	Conventional capture-recapture	Software for making abundance and density estimates using a limited range of conventional capture-recapture models. Inference is based on the models in White *et al*. (1978), rather than modern maximum likelihood estimation.	1978 - 1991	Otis *et al*. (1978)	www.mbr-pwrc.usgs.gov/software/capture.shtml
MARK	Conventional capture-recapture (and mark-resight)	Relatively complex and comprehensive software with a steep learning curve. Also implements occupancy models. Fits models using maximum likelihood methods (unlike CAPTURE), allowing for model selection and hypothesis testing. Good support available from an active community.	1999 - current	Cooch & White (2016)	www.phidot.org/software/mark/downloads www.phidot.org (for help forum)
"RMark" package in R	Conventional capture-recapture (and mark-resight)	The R counterpart to MARK, allowing complex models to be fit using just a few lines of code. With some work, it is possible to get RMark functioning on Mac and Linux (see RMark documentation).	2011 - current		cran.r-project.org/package=RMark
"multimark" package in R	Conventional capture-recapture using multiple marks	Allows for an integrated analysis of data on two individually-identifiable animal marks (e.g. left and right flanks of animals), as might be obtained from capture-recapture surveys which do not use paired cameras. Also implements standard models using a single mark.	2015 – current	McClintock (2015)	cran.r-project.org/package=multimark

Software	Type of analysis	Description*	Years active	Helpful references	Website
DENSITY	Spatially-explicit capture-recapture	Relatively simple software. Software development has now shifted to the R package "secr".	2007 - 2014	Efford *et al*. (2004)	www.landcare research.co.nz/services/software/density www.phidot.org (for help forum)
"secr" package in R	Spatially-explicit capture-recapture (and mark-resight)	Implements the latest developments in spatially-explicit capture-recapture. Much more comprehensive than DENSITY. Cross platform (Windows, Mac and Linux).	2010 - current		cran.r-project.org/package=secr
SPACECAP	Spatially-explicit capture-recapture	Implements spatially-explicit capture-recapture in a Bayesian mode of inference (which is arguably better for small sample sizes). Does not require any programming skills.	2010 - 2014	Gopalaswamy *et al*. (2012)	cran.r-project.org/package=SPACECAP
"oSCR" package in R	Spatially-explicit capture-recapture	Another option for fitting SECR models in R. Implements fewer models than the "secr" R package.	2016 - current		sites.google.com/site/spatialcapturerecapture/oscr-package
"activity" package in R	Random encounter modelling	Currently only activity level estimation is supported, but a complete R package for REM density estimation is on the horizon.	2014 - current	Rowcliffe *et al*. (2014)	cran.r-project.org/package=activity

*Except where noted, programs work only on Windows and are free-to-use.

It will often be necessary to adapt the guidelines we provide here to a given local context. This may require substantial trial-and-error in the field, as well as ingenuity in solving problems.

Camera-trapping a potential burrow of the rare Cuban solenodon, *Atopogale cubana*: © Oliver Wearn

13 MISCELLANEOUS TIPS AND TRICKS FOR CAMERA-TRAPPERS

1. Read the manual. Yes, really. Even though camera trap manuals sometimes sound like they've been Google-translated from English to Finnish to Mandarin and back again, they usually contain some invaluable (and sometimes surprising) insights about your camera.
2. Get a smart charger. It won't make you smarter, but it will save your batteries.
3. Get to know Quantum GIS. And-or R. But then you knew that already.
4. Practice data redundancy. In other words, record everything in multiple ways to avoid losing key information.
5. Find out if your camera traps are covered for damage or theft by your institution's insurance policy.
6. In humid environments, allow your cameras to come to ambient temperature before removing from dry bags / dry boxes / air conditioned rooms, otherwise condensation will quickly build up inside them.
7. Apply masking tape over the flash if using camera traps for close-up work. This will dampen the flash and help avoid over-exposure.
8. Angle the camera lower than you think. The worst that can happen is that you get less sky in your pictures. Unless you want images composed entirely of animal ear-tips, then go ahead.
9. Never smoke and camera trap. The scent of cigarettes will remain on your cameras, scaring off wildlife for weeks, and your life expectancy will be shorter.
10. Try to avoid mixing your food and camera traps, especially if your lunch box is prone to opening spontaneously.
11. Put leaves on the ground in front of the camera to stop mud splashing up onto the lens and sensor in heavy rain.
12. Buy some epoxy resin or silicone sealant to make fixes to damaged cameras on the go.
13. "Copy-and-paste" rather than "cut-and-paste" images from memory cards onto your hard-disk. That way, if the transfer crashes, you don't corrupt any of the images.
14. Format memory cards each time you use them. This sorts out any parts of the memory which might have become corrupted, and usually gives you a bit more memory capacity.
15. Make a "greatest hits" folder at the outset and copy over any good images as you come across them. Otherwise you can guarantee you won't be able to find that image of porcupine copulation ever again.
16. Even better, share your best images hot-off-the-press on social media – the more recent the time-stamp, the more kudos you'll earn.
17. Reach out to the camera-trapping community (e.g. on the Yahoo or WildLabs camera trap groups) if you get stuck. They are a friendly bunch, if a bit distracted (they´ve probably got a million unidentified camera trap images hanging like a dark cloud over their head).

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