Chapter 6

Camera trapping for inventorying terrestrial vertebrates

by

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Abstract

The use of automatic cameras triggered by passing animals (camera trapping) is a fundamental technique to record medium to large mammals and terrestrial birds in the field. Photographs provide objective records, or evidence, of an animal's presence and identity. The method underwent enormous advance and has been increasingly used in the last decade. Besides faunal inventories and assessments of activity pattern, relative abundance and habitat preference, inferential sampling studies using camera traps allow estimations of occupancy and density. As such, camera trapping is a fundamental method for All Taxa Biodiversity Inventory (ATBI) projects. Following an introduction with historical background, we describe the various phases of using camera trapping with ample details on the practical aspects from the choice of camera model and setting of cameras in the field to the analysis of photographs, and storing and management of data. Key study designs and analytical procedures are described, particularly species inventory and occupancy studies, and their application to design monitoring programmes.

Key words: phototrapping, checklist, mammals, survey, occupancy

1. Introduction

Camera trapping refers to the use of remotely triggered cameras that automatically take images of whatever walks in front of them. Most camera trap models are triggered by a passive infrared sensor detecting a moving object warmer than the ambient temperature such as animals, people, or vehicles passing in front of them. Camera trapping is most often used to capture images of medium to large sized terrestrial mammals and birds, but has also been recently used for arboreal mammals (Oliveira-Santos *et al.,* 2008). Camera trapping methodology underwent significant advances and has been increasingly used in the last decade (O'Connell *et al.,* in press). The number of publications per year that investigated or used camera trapping increased from less than five during 1993-2003 to 55 in 2008 (Rowcliffe & Carbone, 2008, using the topic search tool in the Web of Science) and by 2009 has increased to around 150 publications. Camera traps have been used to record fauna in a wide range of habitats, from snow leopard in the Himalayas (Jackson *et al.,* 2006) and bobcat in northern California (Larrucea *et al.,* 2007) to a wealth of studies in the humid tropics (*e.g.* Karanth & Nichols, 1998; Rovero & De Luca, 2007; Tobler *et al.,* 2008a). Camera traps were used to obtain the first pictures in the wild of the Chinese mountain cat (Sanderson, 2007; Yufen *et al.,* 2007) and Abbott's duiker (Rovero *et al.,* 2005), and to detect a new species of giant elephant-shrew (Rovero *et al.,* 2008). Besides their use for carrying out faunal inventories and obtaining information on activity pattern and habitat preference, scientifically robust, inferential sampling studies using camera traps can allow to estimate occupancy and density.

Following a historical background of camera trapping, key advantages of camera traps are presented. Also included is a detailed guide on the use of camera traps. Many useful details are provided, including how to choose a camera trap model and the practicalities of placing camera traps in the field. The analysis of photographs, image management including data storage, and data analysis are also discussed.

History of camera trapping

Camera trapping was invented in the late 1890s by George Shiras III, a Yale-educated lawyer who perfected a way of photographing wildlife at night with a large-format camera and hand-operated flash. Shiras soon gained considerable acclaim for his stunning night photographs of deer and other animals (Sanderson & Trolle, 2005). The first camera trap photos were taken when Shiras set up his camera so that he could take a picture remotely by pulling on a long trip-wire. Eventually, he arranged the trip-wire so that an animal triggered the camera. His articles in *The National Geographic Magazine* from 1906 to 1921 created considerable interest in wildlife photography (Shiras, 1913). Subsequently, in the late 1920s, Shiras taught Frank M. Chapman (a leading ornithologist from the American Museum of Natural History in New York) how to use camera traps for his work in the tropical rain forest of Barro Colorado Island in Panama. Chapman employed Shiras' camera traps to capture images of the diverse and, at that time, poorly known fauna, including tapirs, ocelots and pumas. For many years, Chapman was one of the few researchers to use camera traps. Several decades passed before researcher re-discovered camera traps as a tool. Seydack (1984) was probably the first to use automatic camera traps to study rainforest mammals. He collected data for inventorying species as well as estimate bushbuck abundance and identify individual leopards in Africa. Griffiths & van Schaik (1993) used camera-taps to study rainforest mammals in Indonesia, and realized the potential of this method to detect species presence and study behaviour, activity patterns and abundance of elusive mammals (Griffiths & van Schaik, 1993; van Schaik & Griffiths, 1996). Meanwhile, Karanth employed camera traps to identify individual tigers in Nagarahole National Park, India. His success with applying capture-recapture models to estimate density from camera trap data (Karanth & Nichols, 1998) moved camera trapping towards the realm of science-based, inferential sampling, thus leading the way for camera trapping to become an important tool for quantitative wildlife research (O'Connell *et al.,* in press).

Hunters, especially in the USA, began using camera traps in the late 1990s to search for trophy deer and other big-game species. This created a small industry resulting in an increasing number of camera trap models spanning a range of prices. At the same time, technology advanced quickly and modern camera traps now have water-proof plastic enclosures containing small, “point-and-shoot” film or digital cameras triggered by passive infrared sensors. Over the last few years, digital and video camera traps have begun replacing film cameras and new models are being introduced each year. Thanks to these advances, camera trapping has become a widely used tool in wildlife biology, opening the way to an impressive number of studies (Rowcliffe & Carbone, 2008).

Advantages and efficiency of camera trapping

Camera trapping is a non-invasive method that generally causes a minimum of disturbance to the target species. Camera traps can be left unattended in the field for several weeks, and thus are ideally suited for studying rare, elusive, and nocturnal/crepuscular animals that avoid humans. The big advantage of camera trapping in comparison to other methods used to record medium-sized to large terrestrial mammals (see chapter 19 by Hoffmann *et al.)* is that photographs provide objective records, or evidence, of an animal’s presence and identity. In addition, camera trapping provides information on activity patterns (from the date and time contained in the image), behaviour, and pelage characteristics that enable individual identification.

Various studies show that camera trapping is an efficient method for inventorying the community of medium to large terrestrial mammals, with 57 to 86% of species detected using survey effort of 1035 to 3400 camera trap days (Table 1). A study in Suriname shows that the totality of species can potentially be detected when deploying large survey effort. Survey effort is usually measured as the number of camera traps multiplied by the number of sampling days. For example, an effort of 1000 camera trap days can be obtained using 10 camera traps run for 100 days, or 20 camera traps run for 50 days. However, despite the relatively large proportion of species that can be recorded, some species may not be detected even after several thousands of camera trap days (Tobler *et al.*, 2008a). This has important implications when designing a study because (1) large trap effort does not guarantee survey completeness, and (2) failure to detect a species does not mean the species is absent.

Site	**Number of species (proportion of total)**	**Trap effort (camera days)**	**Source**
Emas National Park, Brazil	16 (57%)	1035	(Silveira *et al.,* 2003)
Atlantic forest, Brazil	17 (81%)	1849	(Srbek-Araujo & Garcia, 2005)
Udzungwa Mountains, Tanzania	44 (80%)	3400	(Rovero & De Luca, 2007)
Los Amigos, Peru	21-24 (75-86%)	1440-2340	(Tobler *et al.,* 2008a)
Bakhuis Mountains, Suriname	27 (100%)	49589	J. Sanderson (in preparation)

Table 1. Efficiency of camera trapping for inventorying medium to large mammals at different sites. Camera days are defined as the number of cameras multiplied by the number of days they were functioning.

2. Guide to the use of camera traps

2.1. Camera traps: choosing the right model

The aim of this chapter is (1) to illustrate how camera traps work, and (2) to give guidelines on how to choose the appropriate cameras trap for a study. With a rapidly growing number of camera trap models available on the market, choosing the right model can often be difficult. Our aim is not to recommend a specific brand or model (as these have a quick turn-over in the market), but rather to describe important criteria for choosing the proper camera trap for a particular study (Table 2). A list of additional resources is given in the Appendix 4.

2.1.1. Trigger mechanism: active and passive sensors

With the exception of active sensor models produced by TrailMaster®, commercially available camera traps use a passive sensor that detects heat-in-motion. The sensor triggers the *image recording device* (henceforth called camera, to indicate any recorder including digital ones) when something warmer than the ambient temperature passes in front of the sensor. Thus, reptiles typically elude detection because their body temperature is close to the ambient temperature.

Active sensors detect objects within a *detection zone* (or opportunity cone). The apex of the zone starts at the small sensor within the camera trap and expands outward from the camera trap in a circle. The detection zone increases with the distance from the sensor but is still much smaller in area or cross-section than the field of view of the camera. As a consequence, the position of the animal in the photo depends on the following important factors: (a) the size of the detection zone, that in turn depends on how close the camera is to the animal (see below), (b) the *trigger speed* (or latency time): the length of time between object detection by the sensor and the camera recording a picture, and (c) the speed of the passing animal.

The main advantage of the passive sensor system is that camera traps are designed as a single unit that can be very small and easy to set, whilst active sensor camera trap systems consist of two or more units (Figs 1,2). A disadvantage is that the various factors described above must be considered when setting the camera trap to ensure that the animals are centred properly in the frame, and that ground heating caused by direct sunlight creates convection waves that can trigger the sensor resulting in empty or “ghost” photographs. Thus, camera traps should not be set at spots with direct sunlight, something that may not always be easy.

An active sensor is similar to a garage door sensor and consists of two components: a transmitter and a receiver (Fig. 2). The transmitter emits a beam of light, typically red, that is detected some distance away by a second component referred to as the receiver. When the beam of light is broken by a passing animal, the detector unit triggers the camera to take a picture. Although active camera traps are employed less frequently than passive camera traps, there are some clear advantages: (1) the beam is typically very narrow so that the subject’s position along the beam can be more precisely anticipated; (2) the camera can be placed independently of the sensor and detector allowing for creative photographs. Ground heating causing heat-in-motion that triggers an active sensor camera trap is not a problem for active sensor systems because the light beam remains unbroken by convection waves. However, a falling leaf can break the beam and cause the camera to record a picture (Table 2).

Fig. 1. Examples of camera-trap images; top left: a jaguar, *Panthera onca*, not centred in the frame (possibly because the animal walked too fast or the camera triggered too late); top right: a leopard *Panthera pardus* centred in the frame and holding a prey (blue duiker *Philantomba monticola*) in its mouth; bottom left: setting a camera-trap pointing to a small wildlife trail in the rainforest of Tanzania; bottom right: nocturnal photo of a bushy-tailed mongoose *Bdeogale crassicauda* taken with a Reconyx® digital camera mounting an infrared flash (photos by F. Rovero and J. Sanderson).

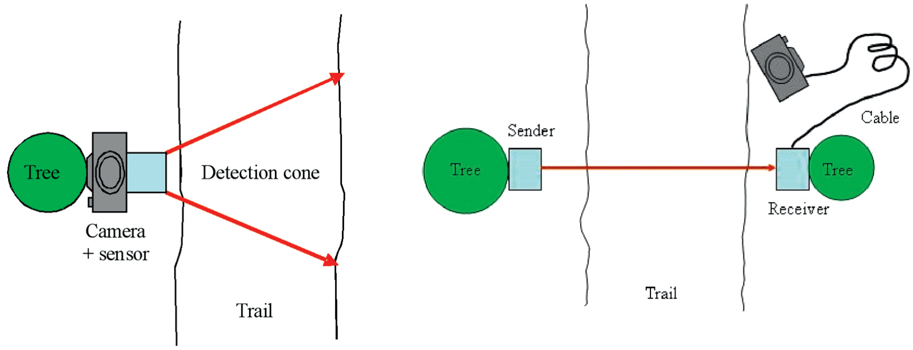

Fig. 2. Schematic figure of passive (left) and active (right) camera-trap systems.

2.1.2. Trigger speed

The trigger speed, or latency time, is the time it takes from the moment the sensor detects an object until the camera takes a photograph. Fast trigger speed is usually preferred for faunal inventories because there may be very few chances to record rare or elusive species. Camera traps set along trails require a faster trigger speed (1/2 second or even 1/10 second), because animals may pass through the frame quickly, whereas camera traps set at mineral licks, baited stations, or under fruit trees can be slower since the animal is likely to pause in front of the camera trap. Trigger speed is often slow in less expensive digital cameras, where it can exceed 2 seconds resulting in many empty photographs. However, most advanced digital cameras, such as Reconyx®, have very fast trigger speed, currently up to 1/10 second.

2.1.3. Camera trap technology: film and digital cameras

Film camera traps use a standard 35 mm film camera, and have been the standard tool used by researchers working with camera traps for the last decade. Over the last few years however, digital cameras have become more widely available, less expensive, and today only a few camera trap manufacturers still make film camera traps. In a few years digital camera traps will likely completely replace film camera traps. Despite this trend, film camera traps might not be replaced altogether so easily, because of their fast trigger speed in comparison to the currently available digital camera traps. Earlier digital camera trap models copied the design of film camera traps with a standard digital camera connected to the motion sensor. Modern digital camera traps usually consist of a camera and sensor integrated on a single board.

The biggest advantage of digital camera traps over film camera traps is that they can store thousands of images on a memory card. This means that cameras can be left in the field for a much longer period of time without the need for checking them. Also, images can be viewed immediately in the field whereas film must first be developed. Data management is more easily achieved with digital photographs that avoid the necessity of scanning film.

Battery life varies greatly among models and, while some camera traps only last a few weeks on a set of batteries, others run for two months or more and can take thousands of photographs. Battery life decreases with the number of photographs taken and cameras with an infrared flash usually have longer battery life than models with a regular flash but are limited to black and white photographs at night. To conserve power, some digital cameras go into a sleep mode after a certain amount of time which can greatly increase the time it takes them to take the first picture. We recommend testing each camera trap in the setting it will be used before investing in a large number of them (Table 2).

Sensor system	**Advantages**	**Disadvantages**
Passive sensor	Single unit Detects animals of a wide range of sizes	Placing the animal in the centre of the frame may be difficult Triggered by heat from sunlight
Active sensor	Subject positioning is precise Heat from sunlight does not activate sensor	Made of 2 or 3 units and more complex setting and programming More expensive
Camera-trap technology	**Advantages**	**Disadvantages**
Film camera	Fast trigger speed for most models, low power requirements	Very few models are still available on the market Must be checked often as film may fill up quickly
Digital camera	Can store many photos Digital images more easy to be managed than prints	Trigger speed is slower for most models Per day power requirement is higher than for film cameras
Digital camera with infrared flash	Animals not scared by flash Much less power consumption	Night photographs are in black and white

Table 2. Advantages and disadvantages of different types of camera traps**.**

2.1.4. Weather-proofing

Camera traps are often deployed in the field for a long time and under harsh conditions. Thus, they must be well-sealed. There is a large difference between models, with some models being simply “rain-proof” while others are highly water-proof and resistant to humidity thanks to a tight seal using o-rings. Researchers have used silicon, tape, and other arrangements to better seal camera traps, however a well-sealed model is much preferred. Often a small package of silica gel or other desiccant is used to absorb moisture inside the camera trap housing.

2.1.5. Cost of camera traps and critical factors to select the model

The cost of camera traps ranges from $50 to more than $800 depending on the model. Camera trap model choice depends on the number of units needed and the total budget. Because performance and characteristics vary between models as explained above, cost alone *should not be* the only criterion by which to choose camera traps. Less expensive camera trap models almost invariably get ruined sooner by the moisture and rain, a slow trigger speed will result in fewer photographs and greater number of animals missed, and if battery consumption is high, then the budget in battery and/or visits to the site for replacing batteries will increase.

Thus, we suggest that three variables be considered to assess cost effectiveness of camera trap models: (1) the cost of the camera traps including batteries, (2) the field costs to visit camera traps for battery/film replacement, and (3) survey duration. The use of high quality rechargeable batteries is a cost-saving strategy if the camera trapping survey is intended to run more than a few months so that the higher cost of rechargeable batteries is recovered. Similarly, if visiting the camera traps is expensive, then more expensive camera traps that generally have longer battery life will minimize the total costs. The ideal strategy to choose among various models would be to test simultaneously different camera traps set at the same sites. With a side-by-side study, and being equal the critical variables of battery life and field costs, then the metric to compare different camera trap models is purely the number of photographs obtained by each camera.

2.2. Setting cameras in the field

2.2.1. Personnel and material needed for setting up cameras

The number of people required to run a camera trap survey depends on the number of camera trap stations, the spacing between camera traps, the frequency with which camera traps are checked, and the accessibility of the stations. These factors depend on the study design (see chapter 3). Some surveys can be carried out by a team of two people while others require four to five people. Local expertise is critical to choosing the most suitable camera trap sites. Much of the work can be carried out by field assistants after careful training but we recommend that a biologist or a technician oversees the survey to manage the data and solve technical problems. Detailed planning is needed before starting field work.

For most surveys, the material needed is as follows:

- camera traps and cables to attach them on trees
- sufficient film/memory card and batteries
- hand-held GPS unit for recording camera trap locations

- data forms (camera trap setting/monitoring and description of camera trap site, see Appendices 1-3)
- flagging tape or tags for marking camera trap locations if necessary.

2.2.2. Preparing the cameras

All cameras should be prepared and tested before going to the field so that they just need to be activated in the field. Check the proper functioning of the sensor and camera by taking test pictures. Carefully inspect all seals to ensure there are no leaks. Dirt on the seal allows water to enter. Each camera trap must be uniquely numbered, or coded, for identification purposes. Write the code with a permanent marker on the housing of each camera trap. Some digital camera traps allow printing the code automatically at the bottom of each photograph. If this is not an option then taking a picture of a whiteboard showing the camera trap code with the date and time is a useful technique. For film cameras this allows identification of rolls of film from the first picture. Write the camera trap code, and start and end date on the outside of the film roll to easily track film from the field to development.

Make sure to carefully set the date and time on each camera. Re-check the date in the field when installing the camera trap. Another critical setting is the sensor sensitivity which for some passive sensor camera traps can be set too low or high. We recommend high sensitivity when working in hot climates and when small species should be photographed. For most camera trap models the time interval between consecutive photos, i.e. the time the camera waits after taking a picture until it takes another picture (the so-called *delay* time), must be chosen. Because repeated pictures of the same individual are often not useful, this setting should be sufficiently long to allow animals to move on. Times between 1 minute and 15 minutes are typically used. If camera traps can store many photos or can be checked frequently, a shorter delay time can be used.

2.2.3. Choosing a site and setting the camera

To maximize trapping success, camera traps are best set along trails. Knowledge on signs of wildlife presence and spots where animals frequently pass can be of great help when choosing camera trap locations. Camera traps are usually attached on a tree or pole at about 50 cm above ground. Once the site is selected, search for a straight tree to attach the camera trap (Fig. 1). If no suitable tree is available, a pole can be used. The tree or the position of the pole should be chosen based on the optimal distance between the camera trap and the point along the trail that will be the centre of the frame. Cameras with fast trigger speed (1/2 second or less) are usually set at about 2 m back from the trail to allow taking picture of a wide range of animals. If the trigger speed of the camera trap is slow, set the camera trap as far as 5-10 m from the trail. Note that small-bodied animals will appear very small in the frame. Camera traps are usually set perpendicular to the trail to obtain a good side image of the passing animal; however, they can also be placed slightly off perpendicular to the trail (i.e., about 60° between camera trap aim and trail) to increase the path length the subject will take through the frame. We recommend some testing with the camera trap to determine the detection zone. This is especially easy with digital models, but even film models often have a sensor test mode (*e.g.* a flashing red led) that allows testing of the detection zone.

It is critically important to clean the ground in front of the camera trap of debris and vegetation that could cover the animal or reflect the flash, causing the image to be overexposed and, for some cameras, triggering the sensor thus producing series of empty images. Clearing the area will also avoid plant regeneration during the time the camera trap is deployed. As shown in fig. 3, obstacles such as branches can be used to guide the animal's path. In this figure, beside a suspected animal trail are four trees A-D. Trees A and D are too close to the trail for the camera trap. Trees B and C offer the best opportunities for good photographs. The camera trap is placed on tree B that is furthest from the trail. The camera trap sensor can still register a subject on the far right side of the trail. In places of possible risk of theft of camera traps, we suggest locking camera traps to the tree. Most models provide cables that can be locked.

A scent lure can be used to attract passing wildlife to the camera trap and position the subject in the ideal place for a photograph. This allows extra time for the camera trap to obtain a good photograph. Lure has been especially useful for carnivores (Trolle & Kery, 2005; Long *et al.,* 2007).

2.2.4. Recording information on camera setting

The exact camera trap location should be recorded using a handheld GPS unit. Also record the following information: camera trap ID number, date and time camera trap starts to operate, camera trap settings, description of the macro- and micro-habitat around the camera trap (see forms in Appendices 1-3).

2.2.5. Checking camera traps

The time interval at which camera traps are checked depends on the battery life and storage capacity of the camera trap model, the expected number of photographs as well as accessibility. Film camera traps may need to be checked as often as every one to two weeks to make sure they do not run out of film. Digital camera traps can store many more images and thus their autonomy depends on the battery life: most models can run for up to one month and those using an infrared flash can run for up to 2 months and store thousands of images. Camera traps will still need to be checked at least once every three to four weeks to detect camera traps that have been moved by animals or have some other problems. When checking camera traps the following data should be written down: number of photographs, whether film or batteries were changed, battery level as well as any observations about the camera (Appendix 2). This can help estimating average battery life and to figure out up to what date a camera trap that failed was working ok. If possible one or two spare camera traps should be taken to replace camera traps that failed. We also recommend checking the date and time setting of each camera trap each time the camera trap is visited.

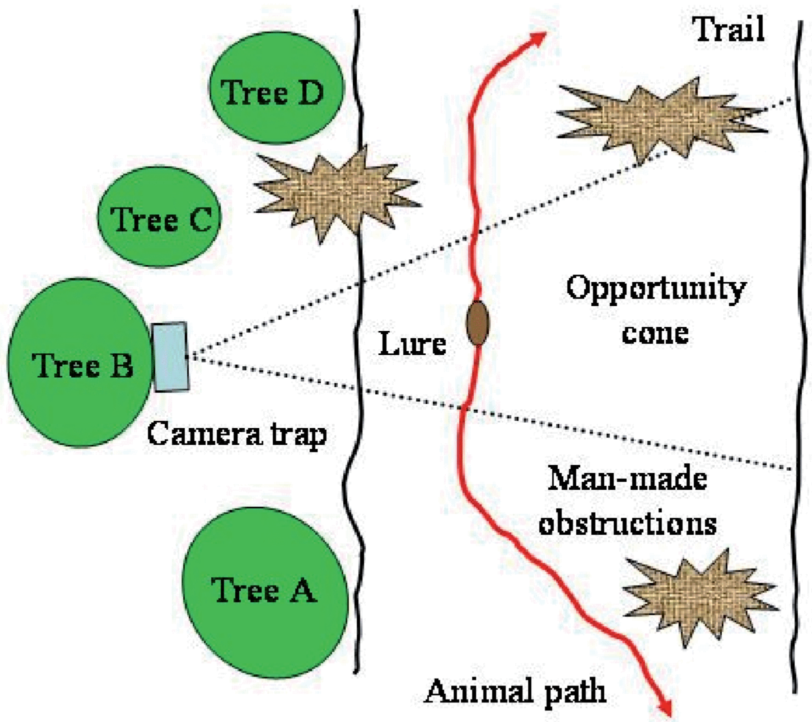

Fig. 3. Schematic drawing of camera-trap positioning, with obstacles placed to maximize the chances that the animal passes at the best distance within the detection zone, or opportunity cone, of the camera.

2.3. Data management

2.3.1. Managing photographs

Camera traps can generate a large amount of data with several thousand images being collected during a large survey. Data should be well organized during all parts of the study to avoid confusion and possibly data loss. Data analysis requires that each photograph has the following information: (1) date, (2) time, and (3) camera trap site code. While the date and time is usually printed on the photograph, only some digital camera traps allow imprinting the camera-trap code on each photograph. For other camera traps, the camera trap code must be tracked throughout the study. Hence we recommend taking a picture of a whiteboard with the camera code, date, and time when setting up the camera trap, and when the changing film or the memory card so that the first and last picture on each roll or memory card contains the proper information. We also recommend writing the code as well as the start and end date on each roll of film.

To manage photographs from film camera traps, several options are available. One option is to get contact sheets with all photographs and then only scan the photos of interests. This will reduce the number of prints required and thereby reduce costs. An alternative is to directly scan all photographs from the negatives. Many photographic laboratories can do this automatically at much lower cost than printing and it is often easier to manage a large number of photographs in digital format. If negatives are scanned, make sure each roll is placed in a different folder. The camera trap code should be entered either as part of the folder name or in a text file in each folder.

2.3.2. Managing data

While the photographs constitute the raw data, the information must be organized in a spreadsheet or database for analysis. The minimum data that must be recorded for each photograph is the code of camera trap that took it, the date and time, and the species that appears in the photograph. Additional information that can be useful is the sex and age of the animal, the number of individuals and comments on the behaviour shown.

Spreadsheet applications (*e.g.* Microsoft Excel) are still the most commonly used software for managing camera trap data. While they are simple to use, their main disadvantage is that organizing data for different analysis can be time consuming. A more flexible alternative is the use of relational databases in the form of either desktop applications (*e.g.* Microsoft Access, Filemaker) or database servers (*e.g.* MySQL, SQL Server). In most cases, the former will be easier to use since they include tools for building forms and queries but the latter might be useful when data is being used and managed by a group of people and must be stored on a central server. Database systems allow images to be linked to the data and all data to be managed in a single system.

Camera Base (http://www.atrium-biodiversity.org/tools/camerabase/) is free software for managing camera trap data. Camera Base is based on Microsoft Access and can manage camera trap data together with the digital images. The software has a wide range of analysis and data export options built-in, including activity patterns, capture-recapture analysis, occupancy analysis, and species accumulation and richness estimation.

3. Study designs

The sampling design appropriate for a specific study depends on many factors: objectives of the study, target species, topography and vegetation, accessibility, number of camera traps to be used, and the time available for a survey. In this section, we will discuss designs suitable for species inventories and occupancy studies. Designs for density estimates using capture-recapture methods, that are applicable to individually-recognizable species, have been discussed in details elsewhere (Karanth & Nichols, 1998; Karanth & Nichols, 2002).

3.1. Species inventory

3.1.1. Objectives

The objective of a species inventory is to obtain a complete list of all species of a certain taxonomic group found in the study area. This list will often be compared to a regional species list and the percentage of all possible species actually found in the area will be used as an indicator for the health of the ecosystem. As described in the introduction chapter, camera trapping has proven to be an efficient tool for detecting terrestrial vertebrates, in particular medium and large sized mammals, and terrestrial birds.

In many monitoring programmes, the most basic measure of interest is species diversity. Species lists however are a poor metric for monitoring large and medium sized mammals. Furthermore, looking only at diversity as an indicator will not detect changes until a species is locally extinct. Thus, methods such as occupancy analysis outlined below will be more appropriate to detect population declines at an earlier stage.

3.1.2. Survey design

For species inventories, single camera traps are set throughout the study areas. The spatial arrangement of camera traps for this study design is flexible. There are no requirements on minimum distances between camera traps or total survey area to be covered. Previous studies showed that the area covered by the camera traps has very little impact on the number of species detected (Tobler *et al.,* 2008a); inventories can therefore be conducted in a relatively small area assuming this is representative of the total study area. However, the even spacing of camera traps allows for more rigorous statistical analysis including occupancy analysis and is generally recommended for monitoring purposes. For example, the terrestrial vertebrate monitoring protocol implemented by the Tropical Ecology Assessment and Monitoring (TEAM) network recommends placing 60-90 camera traps in a grid at a distance of approximately 1.4 km from each other (i.e. one camera every 2 km^2) throughout the study area (TEAM Network, 2008). A list of species expected to be found in the area and some basic knowledge on their natural history is helpful when choosing camera trap locations. The goal is to cover all habitat types of interest and to place camera traps at locations likely to be used by animals. While we recommend setting most camera traps along trails which usually are used by many species, some camera traps can also be set opportunistically targeting specific species that use water holes, mineral licks, streams, dens and fruiting trees.

Unlike surveys designed for capture-recapture analysis where the survey period must be limited to a few months to guarantee population closure, there is no time limit for camera trap inventories. For many sites, the diversity of larger species does not change over a period of a year. Researchers can therefore run a small number of camera traps over many months, or surveys can be spread out over multiple shorter periods throughout a year. Survey effort is usually measured in camera trap days, which is the number of camera traps multiplied by the number of days they operated. In many areas many thousand camera trap days are required to obtain a fairly complete species list (Maffei *et al.,* 2002; Srbek-Araujo & Garcia, 2005; Azlan, 2006; Tobler *et al.,* 2008a); however, as shown in Table 1, efforts in the range of 1,000 to 2,000 camera trap days may be enough for detecting 60-70% of the species. The time needed to carry out a survey is inversely proportional to the number of camera traps used. When using a small number of camera traps we recommend moving camera traps every 15 to 30 days to avoid bias caused by the camera trap locations and to sample a larger area.

If surveys are repeated over years for monitoring species diversity, the same camera trap sites should be used every year, and we recommend running camera traps for approximately the same number of days every year to achieve a comparable sampling effort (TEAM Network, 2008).

3.1.3. Data analysis

Species accumulation curves have been widely used to visually assess the completeness of an inventory and to compare diversity between surveys with different sampling effort (Colwell & Coddington, 1994; Krebs, 1999; Gotelli & Colwell, 2001). They plot the cumulative number of species detected against the survey effort and reach an asymptote when all species have been recorded. Raw species accumulation curves have a stepped shape that makes it hard to detect an asymptote (Fig. 4). This problem is solved by rarefied species accumulation curves which smooth the curve by randomly re-sampling the data and calculating the average number of species expected to be found at a given sampling intensity (Gotelli & Colwell, 2001). While species accumulation curves can be used to compare diversity between different samples, the shape of the curve can vary with the relative abundance of different species (Thompson & Withers, 2003). Communities with a high proportion of abundant species have a steeper initial slope than communities with a high proportion of rare species.

In most surveys some species go undetected even though they are present in the study area. Various methods have been developed to estimate the true number of species from an incomplete survey (Soberon & Llorente, 1993; Colwell & Coddington, 1994; Colwell *et al.,* 2004). For camera trap data non-parametric estimators are usually best suited (Tobler *et al.,* 2008a;b).

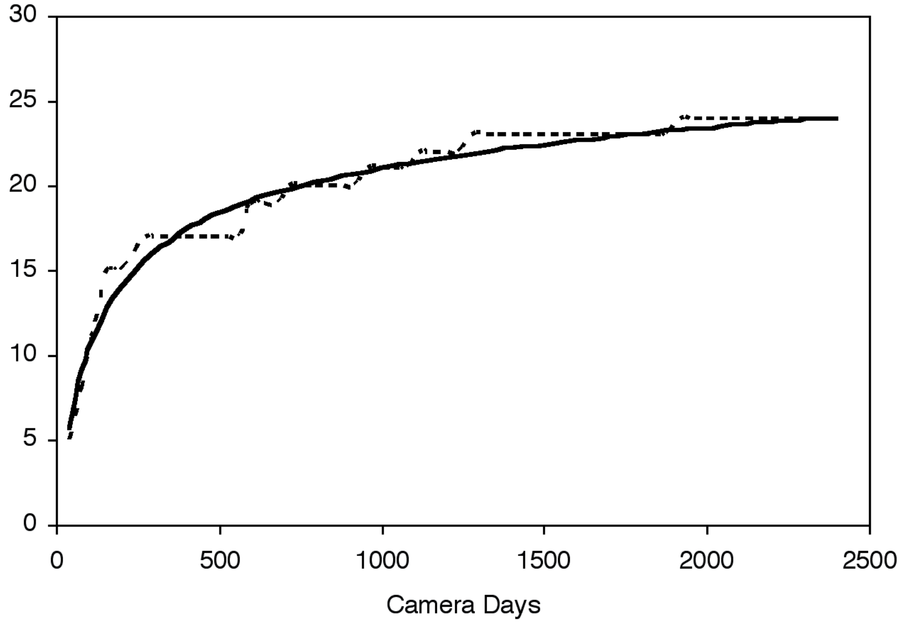

Fig. 4. Raw (dashed line) and rarefied (continuous line) species accumulation curves for camera-trap inventory data from the Peruvian Amazon.

The most commonly used estimators are the abundance-based estimators ACE and Chao 1, and the incidence-based estimators ICE, Chao 2, Jackknife 1, Jackknife 2, Jackknife 3 and Jackknife 4 (Chao, 2004). Jackknife estimators are also used to calculate the M_h model with heterogeneity in closed capture-recapture studies (Otis *et al.,* 1978; Burnham & Overton, 1979) and showed good results for camera trap data (Tobler *et al.,* 2008a). Species accumulation curves and a variety of diversity estimators can be calculated with the software EstimateS (Colwell, 2006). Diversity estimation based on the capture-recapture model M_h can also be calculated in CAPTURE (Rexstad & Burnham, 1991).

When comparing species diversity between sites based on camera trap samples, methods that account for undetected species should be used. Several methods have recently been developed to deal with this problem based on capture-recapture models and hierarchical-models (Nichols *et al.,* 1998b; Williams *et al.,* 2002; Chao *et al.,* 2005; Chao *et al.,* 2006; Kery & Royle, 2008; Royle & Dorazio, 2008). These methods give an estimate of the number of species shared by two samples and the number of species unique to one or the other sample, however they do not allow for the identification of those species.

3.1.4. Monitoring

Species diversity is concerned with the presence and absence of species and changes are defined as local extinction and colonization. Changes in diversity are inferred by comparing species lists from different years. However, in practice detection probabilities for species are often <1 which can lead to erroneous conclusions. For example, if a species was recorded during one sampling period and was present but not recorded during a later sampling period one would falsely classify the species as extinct. On the other hand, if the species was present but not detected during the first period and was recorded during the later period one would falsely record it as a new colonization. Therefore, models that explicitly include detection probability must be used when analyzing changes in diversity over time and space. Nichols *et al.* (1998a) adapted Pollock's robust design capture-recapture model to estimate species turnover from repeated inventories. Further details on this approach can be found in Williams *et al.* (2002). Royle & Dorazio (2008) propose a hierarchical multi-species site-occupancy model to analyze temporal changes in community composition. Application of these models to analyze camera trap data is under development (T. O'Brien, personal communication), and they have great potential for data from multiple sites or multiple years.

3.2. Occupancy study

3.2.1. Objectives

Estimating abundance or density is a difficult and expensive task for many species and biologists often use some measure of relative abundance to compare between sites or to look at changes over time. For camera trap studies, the use of camera trap rates (number of photographs per camera days) is an intuitive, basic proxy for abundance but count data are often a poor index for relative abundance when detection probability is <1 (Gibbs, 2000; but see 3.3 for further discussion). One possible solution for overcoming the difficulties of estimating abundance is to use occupancy as a surrogate for abundance (MacKenzie & Nichols, 2004). Occupancy is defined as the proportion of area, patches or sites occupied by a species (MacKenzie *et al.,* 2006), and MacKenzie *et al.* (2002) developed a model to estimate site occupancy and detection probability based on repeated presence-absence surveys of multiple sites. Using occupancy as a surrogate for abundance works best for species with small (<5 - 10 km^2), well defined home-ranges. In this case, one can assume that each individual can only appear in one camera trap and the camera trap grid takes a representative sample of the whole landscape. If home-ranges are large in comparison to camera trap spacing then one single individual can appear in many different camera traps and there will be little correlation between occupancy and abundance.

With the inclusion of covariates, occupancy models provide a robust statistical framework for testing many scientific hypotheses. For example, one can test for differences in occupancy rates between study sites that contrast by habitat types, hunting levels, distance to key resources, weather conditions, vegetation features. It is also possible to evaluate differences in detection probability between camera models and investigate changes in occupancy over time (O'Connell *et al.,* 2006; Linkie *et al.*, 2007; Tobler *et al.,* 2009). Occupancy models can also be expanded to combine data from different survey methods (*e.g.* track stations, hair traps, live traps) and to look at occupancy at multiple spatial scales (O'Connell *et al.,* 2006; Nichols *et al.,* 2008).

3.2.2. Survey design

When carrying out an occupancy study camera traps should be set out in a regular grid with approximately equal distances between cameras. They should cover all habitat types of interest and the number of camera traps in each habitat type must be sufficiently large to allow for analysis. If possible the distance between camera traps should be larger then the diameter of the average home range of the species of interest, to avoid spatial auto-correlation. If the home-range diameter of a species is much larger than the distance between camera traps the results should be interpreted as the percentage of area used by a species during the survey period instead of the percentage of an area occupied (Tobler *et al.,* 2009).

The survey time needed largely depends on the detection probabilities of the species of interest. The higher the detection probability, the fewer survey days are needed to collect reliable data. Occupancy models assume that occupancy does not change over the survey period and, similar to capture-recapture studies, surveys should therefore be limited to two to three months. If species are known to seasonally migrate in and out of the study area surveys should be conducted outside the migration period.

Occupancy studies require a large number of camera traps to produce reliable data. Simulations showed that to increase the accuracy it is usually more efficient to increase the number of camera stations than to increase the number of survey days. This can be done by setting camera traps in multiple blocks; for example, TEAM protocol recommends deploying three consecutive blocks of 20-30 cameras, each block operating for at least 30 days (TEAM Network, 2008). If preliminary data on capture probability is available one can use the simulation capabilities of GENPRES (Hines, 2007a) or MARK (White, 2009) to estimate the optimal number of survey days and camera trap stations (Bailey *et al.,* 2007).

3.2.3. Data analysis

In this section we will focus on specific issues related to camera trap data. For details on the statistical analysis of occupancy data we refer the reader to the available literature (*e.g.* MacKenzie *et al.,* 2003; Royle, 2004; MacKenzie *et al.,* 2005; MacKenzie *et al.,* 2006). Two software packages are available for data analysis: PRESENCE (Hines, 2007b) and MARK (White, 2009).

Occupancy models use repeated presence/absence surveys to estimate the proportion of sites that are occupied by a species. If we assumed that we can always detect a species when it is present (p=1) then we could simply estimate occupancy by $\hat{\Psi} = x/s$ where x is the number of occupied sites and s the total number of sites sampled. If p<1 then $\hat{\Psi} = x/s/\hat{p}$ where $\hat{p}$ is the cumulative detection probability estimated from the data. Royle & Nichols (2003) extended this model to allow for abundance-induced heterogeneity. The idea behind the

Royle-Nichols (RN) model is that site-specific detection probabilities vary due to differences in the number of individuals present at each site, and using a mixture model these abundances can be estimated from the repeated presence-absence data. In the RN model, the occupancy Ψ is not directly estimated and has to be derived from λ, the average number of individuals at each site as $\Psi = 1 - e^{-\lambda}$. In simulations this model significantly improved occupancy estimates for data with high levels of heterogeneity (Dorazio, 2007).The RN model assumes that populations are closed and that individuals are distributed in spaces according to a Poisson process. If these assumptions are violated, the estimated parameters should not be interpreted as abundance but rather as a random effect (MacKenzie *et al.,* 2006: 141). However, occupancy estimates will still be less biased than under models that don't include heterogeneity.

The first step of data analysis consists in compiling the detection histories for each camera trap station. A detection history consists of 1 and 0 indicating whether the species was detected (photographed) during a sampling occasion or not. For example, a detection history of "01101" indicates that the species was detected during sampling occasion two, three and five. For camera trap data a sampling occasion usually consists of one or multiple consecutive days. For low detection probabilities the maximum likelihood estimator used to estimate parameters often fails to converge. For rare species it is therefore required to combine data from several days into one sampling occasion to increase detection probability. As a general indication, occupancy models will not produce any useful results for species that show up in less than 10-20% of all camera traps and have capture probabilities smaller than 0.1.

In a second step, possible covariates are selected. Covariates can be used for occupancy as well as detection probability and they should be selected based on *a priori* hypothesis to limit the number of different models. To find the model that best fits the data, different models are compared using standard model selection procedures based on the Akaike's Information Criterion (AIC; Burnham & Anderson, 1998; MacKenzie *et al.,* 2006). We suggest comparing a single-season model with the RN model to test for heterogeneity in the data.

3.2.4. Monitoring

Occupancy models have great potential for monitoring species with small and medium-sized home-ranges. While they might not be very sensitive to small fluctuations, they can detect continuous population declines of larger fluctuations. If possible the same study design should be used every year for monitoring programmes. When analyzing multi-year data the survey year can be used as a continuous covariate to detect linear trends or as a discrete covariate to test for differences occupancy between years when occupancy is oscillating. It is also recommended to test for differences in detection probabilities among years. Model selection can be used to test if the model with time (years) as the covariate fits the data better than a model that assumes no change in occupancy over time.

3.3. Other applications

Data obtained from camera trap surveys that are principally aimed at faunal inventories may allow for other important questions to be addressed for selected species. Since each photograph includes the exact time it was taken, camera traps collect detailed data on the activity patterns of many species (van Schaik & Griffiths, 1996; Gómez *et al.,* 2005; Azlan & Sharma, 2006) and can be used to study differences in activity patterns between sympatric species (Jacomo *et al.,* 2004; Di Bitetti *et al.,* 2009; Tobler *et al.,* 2009), or changes in activity related to human impact (Di Bitetti *et al.,* 2008).

Habitat use based on camera trap data has been evaluated in different ways using Chi-square test, ANOVA and correlation coefficients (*e.g.* Moruzzi *et al.,* 2002; Augustine, 2004; Jacomo *et al.,* 2004; Di Bitetti *et al.,* 2006; Bowkett *et al.,* 2008; Di Bitetti *et al.,* 2009). Most of these studies used the number of photos or a related measure as an index and did not address the issue of detectability. Occupancy models have recently been applied for studying habitat use with camera trap data (MacKenzie *et al.,* 2005; O'Connell *et al.,* 2006; Linkie *et al.,* 2007; Tobler *et al.,* 2009). These models have the advantage that they explicitly include the detection probability allowing to differentiate between factors affecting detection probability and factors affecting occupancy probability (MacKenzie *et al.,* 2006). With an appropriate study design (see 3.2) these models allow researchers to model habitat use based on multiple variables and determine the factors that most influence the distribution of a species.

For some species, data may allow for density estimates to be derived. As mentioned above, for species with individual markings, such as most felids, density estimation can be derived using capture-recapture analysis (Karanth & Nichols, 1998). Rowcliffe *et al.* (2008) proposed a method to estimate density without the need for individual recognition, based on modelling the contacts between cameras and animals. This method requires parameters such as speed of movement or day range that may not be available for most wild animals. As an alternative method, camera trap rates can be used as a surrogate for abundance for species that cannot be identified from images. A recent study on rainforest ungulates shows the validity and usefulness of this index (Rovero & Marshall, 2009). The relationship between trap rate and true abundance must be assessed through calibration with independently-derived density estimates (O'Brien *et al.,* 2003; Rovero & Marshall, 2009), making this index of less simple use than it may seem. Calibration should ideally be re-assessed periodically and when comparing camera trap rates across contrasting sites (O'Brien, in press).

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5. Appendices

Appendix 1. Camera-trap deployment form

Camera ID code	Camera position (Lat/long)	Start year, day, time	Notes	Recorder name

Appendix 2. Camera-trap monitoring form

Camera ID code	Year, day, time	Film Changed	Battery Changed	Number of photos taken	Notes	Recorder name
		□	□			
		□	□			
		□	□			
		□	□			
		□	□			
		□	□			
		□	□			
		□	□			

Appendix 3. Camera-trap site habitat description form

Study site…………………….. Date………………………………
Data collector………………………….

Camera ID number………… Nearest cameras and approx distance……………………………………………

Altitude (m a.s.l.)………. Slope (deg.)……………......

Distance to nearest village/park boundary………………………..

Camera placed on: large trail small trail Other…………………

Bait used: ……………………… Any signs/dungs already in site……………………

Gross habitat: lowland forest submontane forest montane forest swamp regenerating forest riverine plantation woodland bamboo grassland cultivation

Other habitat…………………..…..

Canopy cover (for forest habitats): closed canopy regenerating shrubby open
Floor cover: shrub/thickets > 2m height < 2m seedlings grass leaf litter rock
Cover density dense moderately dense open

Dominant tree species………………………………………………………………

Dominant understorey species……………………………………………………

Any further relevant description (*e.g.* more details on microhabitat)…………………………………………………………………………
……………………………………………

Appendix 4. Useful web-sites

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

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

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

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

http://www.chasingame.com/
Detailed reviews on many different digital camera-trap models.

A selection of camera-trap producers' web-sites:

http://www.reconyx.com/
http://www.trailmaster.com/
http://www.snapshotsniper.com/
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